Ecology of the Black-faced Sheathbill on Marion Island

by

Gregory T.W. McClelland

Submitted in partial fulfilment for the degree

Doctor of Philosophy in Zoology

Centre for Invasion Biology

Department of Botany and Zoology

Faculty of Science

Stellenbosch University

Supervisor: Prof. Steven L. Chown

Co-supervisor: Ass. Prof. Res Altwegg

August 2013

Declaration

By submitting this thesis/dissertation electronically, I declare that the entirety of the work contained therein is my own, original work, that I am the sole author thereof (save to the extent explicitly otherwise stated), that reproduction and publication thereof by Stellenbosch University will not infringe any third party rights and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

Date: August 2013

Abstract

As the pace of climate change has begun to accelerate so too has it become clear that the direct impacts thereof are likely to have profound consequences for many island systems. Moreover, it has also been suggested that climate change will exacerbate the effects of many invasive species, so further impacting both diversity and ecosystem functioning. Forecasts for such interactions have been most pronounced for the Southern Ocean islands, which are home to a wide variety of endemic species. This thesis is about such interactions and their specific impacts on a key endemic, the black-faced sheathbill (*Chionis minor*) on the Prince Edward Islands.

Of increasing concern is how invasive rodent populations in the Southern Ocean may be responding to global climate change, as ameliorating conditions on these islands are forecast to decrease thermal and resource restrictions on rodents. However, firm evidence for changing rodent populations in response to climate change, and demonstrations of associated impacts on the terrestrial environment, are entirely absent for the region. In Chapter 2 of this thesis, these relationships are explored for invasive house mice (*Mus musculus*) on Marion Island. Using spatially explicit capture-recapture modeling, it is determined that mouse populations across a range of habitats have increased over time. Owing to an extended breeding season, made possible by ameliorating conditions brought on by climate change, the total number of mice on the island at annual peak density more than doubled over the past decade. It is also demonstrated that mice directly reduce invertebrate densities, with biomass losses up to two orders of magnitude in some habitats. Because of the importance of invertebrates to nutrient cycling on the island, such changes are likely to have significant ecosystem-level impacts.

In Chapter 3 the focus expands to examine how increasing mouse impacts and other outcomes of climate change are affecting the ecology of the black-faced sheathbill. It has been established that invasive house mice are capable of suppressing the populations of several seabird species in the Southern Ocean. However, mouse impacts on the region's few island endemic land-birds remain largely unexplored. Further, a significant effect of climate change may be realized by altering interspecific interactions, specifically food webs. A significant portion of sheathbill diets is derived from rockhopper penguins, a species currently under a climate-change-driven decline, which may have significant effects on sheathbills. The study found that terrestrial invertebrates are no longer a significant prey

resource for sheathbills on Marion Island, and that sheathbills have effectively been displaced from a formerly important winter food resource by mice. In response, the number of sheathbills foraging in king penguin colonies increased. Moreover, a reduced rockhopper penguin population lead to significant declines in both the number and proportion of sheathbills foraging in rockhopper penguin colonies. The sum result was a significant decline in the body condition of female sheathbills. Rather than decrease reproductive output, sheathbills responded by decreasing clutch size and producing significantly fewer male nestlings. While population estimates did not detect a reduction in the number of sheathbills, population projections suggest that the population is in decline, with the reproductive population declining faster than the absolute population.

There is need for greater study of island species, as for even relatively well-studied taxa such as birds many aspects of ecology remain significantly less studied when compared to species occurring on continents. For example, basal metabolic rate (BMR) is a fundamental characteristic of all endotherms, yet only a handful of island birds have had their BMR measured, and fewer still to a level that allows intraspecific analysis. In Chapter 4 the BMR of black-faced sheathbills on Marion Island was measured to determine whether the unique phylogenetic position and ecology of sheathbills equate to a unique BMR when allometrically compared to other birds. It was found that the BMR of sheathbills is typical for a bird of its size. However, significant intraspecific variation was found to occur, with differences in habitat quality a likely driver.

The results of the study show that the combined effects of climate change and invasive species can have significant consequences for terrestrial endemics in the Southern Ocean. Further, the long-term changes observed in sheathbills make clear the need for improved documentation and study of island species in general, as many of the responses observed in this study are significant but subtle and would not have been evident without detailed knowledge of species ecology and vital rates. Giving greater focus to insular biota is imperative to understanding their current status and ecology as well as establishing a barometer against which further global change can be measured and mitigation measures evaluated.

Specific conservation responses for the black-faced sheathbill on Marion Island include the provision of nest boxes at king penguin colonies, and eradication of house mice.

The latter would have long-term benefits for the species, invertebrates, ecosystem functioning generally, and likely also for important seabirds such as several species of albatrosses whose chicks are being increasingly preyed on by mice. Eradication would, however, be difficult and expensive, and with substantial potential non-target effects, including on sheathbills, that would have to be carefully managed. In the absence of local mouse eradication, and with ongoing climate change, specific management of the sheathbill population through the provision of supplementary nesting sites seems the most appropriate conservation action. It should therefore be examined in small-scale trials to ascertain the likelihood of unintended consequences. Importantly, the maintenance of Prince Edward Island as largely free of invasive species is key to the conservation of the local black-faced sheathbill subspecies, *Chionis minor marionensis*, endemic to the Prince Edward Island group.

Opsomming

Soos die tempo van klimaatsverandering begin om te versnel, het dit ook duidelik geword dat die direkte impak daarvan waarskynlik ernstige gevolge vir baie eilande gaan hê. Verder word dit is ook voorgestel dat klimaatsverandering die gevolge van baie indringerspesies sal vererger, so ’n verdere impak het op beide diversiteit en die funksionering van die ekosisteem. Voorspellings vir sulke interaksies is die meeste uitgespreek vir die Suidelike Oseaan-eilande, wat ook die tuiste van 'n wye verskeidenheid van endemiese spesies is. Hierdie tesis is oor sulke interaksies en hul spesifieke impak op 'n sleutel endemiese spesie is, die swart gesig skedebek (*Chionis minor*) op die Prince Edward-eilande.

’n Groter bron van bekommernis is hoe uitheemse knaagdier bevolkings in die Suidelike Oseaan kan reageer teenoor globale klimaatsverandering, aangesien toestande op die eilande voorspel word om hitte en hulpbron beperkings vir knaagdiere te verminder. Maar, ferm bewyse vir die verandering van knaagdier bevolkings in reaksie op klimaatsverandering, en demonstrasies van gepaardgaande impakte op die terrestriële omgewing, is heeltemal afwesig vir die streek. In Hoofstuk 2 van hierdie tesis, word hierdie verhoudings ondersoek vir indringende huis muise (*Mus musculus*) op Marion-eiland. Ruimtelik vang-terugvang modelle word gebruik om vas te stel dat die muis bevolkings oor 'n verskeidenheid van habitatte mettertyd toegeneem het. As gevolg van 'n uitgebreide broeiseisoen as gevolg van die verligting van toestande gebring deur klimaatsverandering, het die totale aantal muise op die eiland by die jaarlikse hoogtepunt digtheid meer as verdubbel oor die afgelope dekade. Dit is ook getoon dat muise die digtheid van ongewerweldes direk verminder het, met biomassa verliese tot twee ordes in sommige habitatte. As gevolg van die belangrikheid van die ongewerweldes vir voedingstof sirkulering op die eiland, behoort sulke veranderinge waarskynlik 'n beduidende ekosisteem-vlak impak te hê.

In Hoofstuk 3 word die fokus verbreed om te sien hoe die verhoging van die muis impakte en ander uitkomste van klimaatsverandering die ekologie van die swart gesig skedebek beïnvloed. Daar is vasgestel dat indringende huis muise in staat is om die bevolkings van verskeie spesies seevoëls te onderdruk in die Suidelike Oseaan. Maar die muis impak op die streek se paar eiland endemiese land voëls bly grootliks onverken. Verder kan 'n beduidende uitwerking van klimaatsverandering verwesenlik word deur die wysiging

van interspesifieke interaksies, veral voedselwebbe. 'n Beduidende gedeelte van skedebek dieet word gekry van Geelkuifpikkewyne, 'n spesie wat tans onder 'n klimaat-verandering-gedrewe agteruitgang is, wat ook 'n beduidende uitwerking het op die skedebek. Die studie het gevind dat terrestriële ongewerweldes nie meer 'n beduidende prooi hulpbron vir die skedebek op Marion-eiland is nie, en dat die skedebek effektief is verplaas uit 'n voorheen belangrike winter kos hulpbron deur muise. In reaksie hierop het die aantal skedebekke wat kos soek in die koning pikkewyn kolonies toegeneem. Verder, 'n verlaagde Geelkuifpikkewyn bevolking lei tot 'n beduidende afname in beide die aantal en persentasie van skedebekke wat kos soek in Geelkuifpikkewyn kolonies. Die gevolg was 'n beduidende afname in die liggaamstoestand van die vroulike skedebekke. Eerder as ’n afname van reproduksie, het skedebekke gereageer deur 'n vermindering in die aantal eiers en produseer aansienlik minder manlike kuikens. Terwyl bevolking skattings nie 'n afname in die aantal skedebekke kan vind nie, dui bevolking projeksies daarop dat die bevolking besig is om af te neem, met die voortplanting bevolking wat vinniger daal as die absolute bevolking.

Daar is 'n behoefte vir 'n groter studie van eiland spesies, omdat selfs vir betreklik goed bestudeerde groepe soos voëls baie aspekte van die ekologie aansienlik minder bestudeer bly in vergelyking met spesies op die vastelande. Byvoorbeeld, basale metaboliese tempo (BMT) is 'n fundamentele kenmerk van alle endotermiese diere, maar net 'n handjievol van die eiland voëls het hul BMT laat meet, en nog minder tot 'n vlak wat dit moontlik maak intraspesifieke analise. In Hoofstuk 4 was die BMT van die swart gesig skedebek op Marion-eiland gemeet om te bepaal of die unieke filogenetiese posisie en ekologie van skedebekke gelyk aan 'n unieke BMT wanneer allometries vergelyk word met ander voëls. Daar is gevind dat die BMT van skedebekke tipies is vir 'n voël van sy grootte. Daar is egter belangrike intraspesifieke variasie gevind, met verskille in habitat kwaliteit as 'n waarskynlike verduideliking.

Die resultate van die studie toon dat die gekombineerde effek van klimaatsverandering en indringerspesies beduidende gevolge vir terrestriele inheemse spesies in die Suidelike Oseaan kan hê. Verder maak die lang-termyn veranderinge waargeneem in skedebekke dit duidelik dat die behoefte aan verbeterde dokumentasie en studie van die eiland spesies in die algemeen, omdat baie van die reaksies waargeneem in hierdie studie betekenisvol is, maar subtiel en sou nie gewees het sonder gedetailleerde kennis van die spesies ekologie van die spesie nie. Om ’n groter fokus op die insulêre biota te

plaas is noodsaaklik om hul huidige status en die ekologie te begryp, sowel as om 'n barometer waarteen verdere globale verandering gemeet kan word en versagtende maatreëls geëvalueer.

Spesifieke bewaring antwoorde vir die swart gesig skedebek op Marion-eiland sluit in die voorsiening van nes bokse by koning pikkewyne, en die uitwissing van huis muise. Laasgenoemde sou lang-termyn voordele vir die spesie en ongewerweldes hê, asook funksionering van die ekosisteem in die algemeen, en waarskynlik ook vir belangrike seevoëls soos verskeie spesies van albatrosse wie se kuikens toenemend geëet word deur muise. Uitwissing sou egter moeilik en duur wees, en het 'n aansienlike potensiaal vir nie-teiken effekte, insluitend op skedebekke, wat sal versigtig moet bestuur word. In die afwesigheid van plaaslike muis uitwissing, en met voortdurende verandering van die klimaat, spesifieke bestuur van die skedebek bevolking deur die voorsiening van aanvullende broeiplekke blyk die mees geskikte bewaringsaksie. Dit moet dus ondersoek word in 'n klein-skaal proewe om die waarskynlikheid van onbedoelde gevolge te bepaal. Wat belangrik is die instandhouding van Prince Edward Eiland as grootliks vry van indringerspesies en is die sleutel tot die bewaring van die plaaslike swart gesig skedebek subspesie, *Chionis minor marionensis*, endemies aan die Prince Edward Eiland groep.

Acknowledgements

Firstly, a word of thanks to my academic co-supervisors, Steven Chown and Res Altwegg. I am grateful to Steven for the opportunity to study and work on such remarkable islands and for providing much guidance and insight throughout this journey. I have learnt much from our collaboration and your passion for science contributed greatly to my development as a researcher. The significant progress I have made in the daunting world of population modelling is due almost entirely to Res' patient one-on-one instruction and discussion, without which I would have been completely lost. I am greatly indebted to you both.

The field work required to complete this project was exceptionally challenging and could not have been completed without the tireless efforts of several field assistants. For committing themselves to walking enough kilometres in a year to traverse several countries, working in freezing rain past midnight when others were enjoying a movie or warm bed, and subjecting themselves to the ecological phenomenon that is sheathbill excrement, I thank and commend James Wilshere, Mashudu Mashau, Asanda Phiri, Allen Tsautsau, and Matt Lachenicht.

My diverse and interesting colleagues in the CIB, past and present, have been an important part of the PhD for me. They provided friendship and advice that broadened my experience of South Africa and the sub-Antarctic despite me being a "dodgy Canadian". Thank-you to Jessica Allen, Brigitte Braschler, Susanna Clusella-Trullas, Bernard Coetzee, Sarah Davies, Tanya Haupt, Charlene Janion-Scheepers, Jen Lee, Amy Liu, Candice Lyons, Mashudu Mashau, Tshililo Ramaswiela, Andrew Rogers, Pete Le Roux, Justine Shaw, Di Spear, John Terblanche, and Anne Treasure. For their patience and willingness to help I am indebted to Erika Nortje, Mathilda van der Vyver, Karla Coombe-Davis, and especially Anél Garthwaite whose job was not made easier by my incompetence in all things related to paperwork. Elrika Marais was extremely helpful with input on the respirometry setup. My thanks go to the M65 and M67 overwintering teams for being my Marion Island family and sharing in such an amazing experience. The Stellenbosch University International Office, especially Linda Uys, was very helpful in keeping me from being deported before the completion of the thesis.

Alan Burger, Onno Huyser, John Cooper, Rob Crawford, Rudi van Aarde, and Peter Ryan generously shared their data and knowledge of mice and sheathbills and were an invaluable resource that made the project possible.

For financial and logistical support I thank South African National Antarctic Program and the DST-NRF Centre of Excellence for Invasion Biology. I thank the Oceans and Coasts branch of the Department of Environmental Affairs for generously providing unpublished data and field assistance whenever it was requested. I also thank the Department of Botany and Zoology, Stellenbosch.

Lastly, I would like to thank Dad, Mom, Stacey, Jeremy, Abigail, and Millie. Their love and encouragement has allowed me to pursue a life I never thought possible.

Table of Contents

Chapter 1 – General Introduction

"As we neared the beach we saw a bird like a small white hen, eying us inquisitively from the black rocks, against which a considerable swell was washing. This bird was the 'Sheath-bill' (Chionis minor) of which afterward we saw so much" **– H.N. Mosely, Marion Island, 1879**

Black-faced sheathbill (*Chionis minor marionensis*),
King Penguin Bay, Marion Island

Islands

Island ecosystems have proven instrumental in our understanding of both evolutionary and ecological systems and patterns (Losos and Ricklefs, 2009) and are home to many distinct species and assemblages (Carlquist, 1974; Stuart et al., 2012). Species that manage to colonize islands encounter novel ecosystems and increased ecological opportunity (Yoder et al., 2010). With sufficient time and isolation, such conditions may lead to diversification, largely through adaptive radiation (Darwin, 1859), and high levels of endemism can occur (Grant, 1998; Schluter, 2000). As such, islands are home to a disproportionate percentage of global biodiversity (Myers et al., 2000; Kier et al., 2009). Unfortunately, many of the same forces that promote endemicity also leave insular biota remarkably vulnerable to anthropogenic disturbance (Sadler, 1996; Cronk, 1997). As a result, most of the world's contemporary extinctions have occurred on islands (Honegger, 1981; Alcover et al., 1998; Szabo et al., 2012) and they remain the sites of most threatened species (Vié et al., 2008).

Despite being centres for endemic species richness (Kier et al., 2009), islands are generally species poor in comparison with continental areas of similar size and climate (Wallace, 1881; Whittaker and Fernández-Palacios, 2007; Kreft et al., 2008, but see Kalmar and Currie, 2007). As first outlined by MacArthur and Wilson's (1967) equilibrium theory of island biogeography, the number of species on islands is the product of a dynamic equilibrium between isolation-dependent colonization and area-dependent extinction, and larger and/or better connected islands will contain more species than those that are smaller and more isolated (MacArthur and Wilson, 1967). The theory has since been extended to include speciation (Johnson et al., 2000; Whittaker et al., 2008; Chen and He, 2009) and additional work has found that many additional factors such as topography, geologic age, climate, habitat diversity, and community assemblage all interact to contribute to patterns of richness (Schoener and Spiller, 1996; Ricklefs and Lovette, 1999; Losos and Schluter, 2000; Kalmar and Currie, 2006; Whittaker and Fernández-Palacios, 2007; Kreft et al., 2008). Because colonization of islands favours species with high dispersal capabilities, many islands display taxonomic disharmony, where a variety of taxa, including non-volant mammals, amphibians, and freshwater fish and insects, are routinely absent (Baur, 1891). Disharmony plays a significant role in shaping the evolutionary path of island biota. For instance, in the absence of vertebrate grazers, many insular plants lack the structural, morphological, and chemical defences of their continental forbearers (Bowen and Van Vuren, 1997, but see

Terborgh, 2009). Likewise, native fauna often display reduced predator awareness in the absence of vertebrate predators (Williamson et al., 1989). Another common characteristic of island species is lower genetic variability associated with founder effects and small population sizes (Frankham, 1995). Low dispersal ability has also been cited as more prevalent among insular species (Darwin, 1859; Carlquist, 1974) and such patterns appear to be supported for birds (Roff, 1994), plants (Cody and McC. Overton, 1996), and at least in the Antarctic and sub-Antarctic regions, insects (Gressitt and Weber, 1959; Carlquist, 1966; Gressitt, 1970; Crafford et al., 1986; Schermann-Legionnet et al., 2007, but see e.g. Darlington, 1943; Roff, 1990; Denno et al., 2001 for reviews of other regions).

Island birds

The forces that shape island endemic avifauna are often island-specific and depend on such factors as climate, isolation, island area, elevation, and competition and predation (Grant, 1965; Schluter, 1988; Ricklefs and Lovette, 1999; Kalmar and Currie, 2007). But insular selection pressures have lead to several general characteristics within island birds. For example, many islands offer permanent habitat with a local year-round food supply and the absence of predation. Under such conditions the advantages of sedentariness increase as the advantages of dispersal decrease and a reduction in flight capabilities is common (McNab, 1994). A correlation between loss of flight capability and a decrease in basal metabolic rate has also been found: a potential adaptation to the limited resource base often encountered on islands (McNab and Ellis, 2006). Changes in body size compared to mainland counterparts are also prevalent, though whether a general trend exists (the island rule; Van Valen, 1973) is contentious both in general (Lomolino, 2005; Meiri et al., 2008) and when applied specifically to birds (Clegg and Owens, 2002; Cassey and Blackburn, 2004).

Insular avifauna may also show changes in life-history traits in comparison with mainland species. For example, island birds often have broader ecological niches (Lack and Southern, 1949; Cox and Ricklefs, 1977; Scott et al., 2003; Clegg, 2009). Niche expansion reduces the number of conspecifics that a given individual will compete with (Roughgarden, 1972; Dayan and Simberloff, 2005; Svanbäck and Bolnick, 2007) and results in an increase in population size (Van Valen, 1965). Island birds may also show a change in reproductive strategy, often reflective of adaptation to resource limitation, such as lower fecundity and clutch size and higher adult survivorship (Blondel, 2000). Greater investment in offspring,

with longer development periods is also prevalent (Covas, 2012). Such adaptations have allowed island birds to be remarkably resilient to natural disasters capable of devastating entire island populations such as drought, fire, and severe storms. Indeed, the fossil record has yet to reveal a major loss of island birds from natural causes (Steadman, 1995, 2006).

Threats to island birds

Since 1500, the extinction rate for island birds is 40 times higher than for those on continents (Johnson and Stattersfield, 1990), accounting for an estimated 89.3% of known species extinctions and 76.8% of known subspecies extinctions (Szabo et al., 2012). Holocene fossil evidence suggests substantially greater losses prior to European exploration (Olson and James, 1982; Milberg and Tyrberg, 1993; Steadman, 1995; Curnutt and Pimm, 2001; Duncan et al., 2013). The extreme rate of avian extinction is causally linked to the direct and indirect effects of human colonization and visitation (Biber, 2002; Blackburn et al., 2004; Pimm et al., 2006). The same traits that island birds have evolved to be resistant to natural disturbance have left them sensitive to human-mediated disruption. Endemism in of itself is strongly associated with extinction risk (Simberloff, 1994), and common attributes such as flightlessness, ground nesting, larger body size, and naïveté to predators all increase a species' susceptibility to anthropogenic disturbance.

Though island birds may be subject to a variety of threats, numerous studies have identified the introduction of invasive alien species as a primary agent of insular population reductions and extinctions either through direct predation (Atkinson, 1985; Savidge, 1987; Holdaway, 1999; Courchamp et al., 2003; Blackburn et al., 2004; Duncan and Blackburn, 2004, 2007; Towns et al., 2006; Wanless et al., 2007; Jones et al., 2008) or habitat alteration through herbivory (Coblentz, 1978; King, 1985; Morin and Conant, 1998; Donlan et al., 2002; Bergstrom et al., 2009; Brodier et al., 2011). Such devastating and simple ecological effects have rightfully been given much prominence. By contrast, less focus has been given to more subtle interactions. It has become increasingly apparent that invasive species can influence native biotas through more complex and indirect means (White et al., 2006; Simberloff, 2009; Russell, 2011). Prominent examples of indirect effects include mutualism disruption (Lammers and Freeman 1986; Robertson *et al.* 1999; Delgado García 2002), trophic cascades (Schoener and Spiller 1999; O'Dowd et al. 2003; Kurle et al. 2008), and exploitative

competition (Case, 1996; Hansen et al., 2002; Harris and Macdonald, 2007; Ruffino et al., 2008).

Further, as the pace and effects of climate change have begun to increase (Cox et al., 2000; Rignot and Kanagaratnam, 2006; Hansen et al., 2012) so too has it become clear that the direct impacts thereof are likely to have profound consequences for many island systems (Bergstrom and Chown, 1999; Benning et al., 2002; Ingram and Dawson, 2005). Moreover, while interactions between climate change and invasive species are poorly understood, it has been suggested that climate change will exacerbate the effects of many invasive species, so further impacting both diversity and ecosystem functioning (Dukes and Mooney, 1999; Chown and Convey, 2007; Walther et al., 2009). Forecasts for such interactions are most pronounced for more temperate systems, where climate change is expected to create ameliorating conditions that may increase the establishment ability of invasive species, or allow already established species to increase in number and local range, or out-compete native species less adapted to new environmental conditions (Cannon, 1998; Hellmann et al., 2008; Tylianakis et al., 2008). Evidence in support of such forecasts is accumulating (Stachowicz et al., 2002; Chown et al., 2007; Janion et al., 2010), though the number of empirical studies remains relatively limited (Brook, 2008; Walther et al., 2009; Sorte et al., 2013).

Island birds, rodents, and climate change in the sub-Antarctic

Among the greatest threats to birds in the sub-Antarctic is the potentially devastating impact of rodents. Invasive rodents are globally responsible for a large number of island bird extinctions and population reductions (Atkinson, 1985; Towns et al., 2006; Jones et al., 2008) and have been introduced to most Southern Ocean islands (Angel et al., 2008). While much focus has rightfully been devoted to *Rattus* spp., with successful eradication campaigns on several sub-Antarctic islands (Towns and Broome, 2003; Lorvelec and Pascal, 2005), it is becoming increasingly apparent that house mice (*Mus musculus* Linnaeus) are also capable of suppressing the populations of several seabird species (Angel and Cooper, 2006; Wanless et al., 2009, 2012). However, despite such well-documented effects, mouse impacts on the region's few island endemic land-birds remain largely unexplored. While It has been suggested that mice may have negative effects either through competition (Huyser et al., 2000; Imber et al., 2005; Miskelly et al., 2006), or predation (Cuthbert and Hilton, 2004),

such interactions remain speculative. What is clear is that mice are capable of a broad range of impacts in the Southern Ocean, with the potential to alter entire terrestrial ecosystems (Crafford, 1990; Chown and Smith, 1993; Jones et al., 2003; Angel et al., 2008; Phiri et al., 2008), and are thus a potential threat to all endemic species, including island birds.

Of increasing concern is how rodent effects in the Southern Ocean may be changing, as the interactions between invasive species and climate change are predicted to have significant impacts in the sub-Antarctic (Chown and Convey, 2007). Most islands in the region are showing a strong trend towards warming and drying (Jones, Chown, Ryan, et al., 2003; Convey, 2006; Thost and Allison, 2006; le Roux and McGeoch, 2008; Cook et al., 2010; Lebouvier et al., 2011), and concomitant changes in the colonization, distribution, abundance, and impact of several invasive species have been recorded (Bergstrom and Chown, 1999; Frenot et al., 2005; Lee et al., 2007; Lebouvier et al., 2011; le Roux et al., 2013). The considerable impact of rodents on these islands are forecast to be compounded by climate change (Bergstrom and Chown, 1999; Frenot et al., 2005; Convey, 2010). However, firm evidence for changing rodent populations that are, at the very least, significantly correlated, in the expected direction, with climate change are entirely absent for the region. Thus, there is a clear need to assess both how rodent populations are responding to climate change in the sub-Antarctic, and how such changes may affect island ecosystems.

In the sub-Antarctic, Marion Island, of the Prince Edward Island group, presents an ideal opportunity to empirically document the interactions between endemic birds, invasive rodents, and climate change. Invasive house mice on the island have been studied for several decades and have increasingly been found to have significant ecosystem effects (Rowe-Rowe et al., 1989; Crafford, 1990; Chown and Smith, 1993; Smith et al., 2002; Phiri et al., 2008). The Marion Island population of the endemic black-faced sheathbill (*Chionis minor marionensis* Reichenow) has been studied over the same period and there is concern the population may be negatively affected by invasive mice (Smith and Steenkamp, 1990; Huyser et al., 2000). The winter foraging ecology of black-faced sheathbills markedly changed between the 1970s and 1990s, possibly due to exploitative competition with mice for terrestrial invertebrate prey (Huyser et al., 2000). However, while short-term data suggests that such changes to the sheathbill environment have led to a population decline

(Huyser et al., 2000), demographic analysis is lacking and the status of the population is unknown.

Study species: The black-faced sheathbill

Though often referred to in the past as the lesser sheathbill, this thesis will refer to *Chionis minor* as the black-faced sheathbill as recommended by the International Ornithological Congress (Gill and Wright, 2006). The black-faced sheathbill (Fig. 1) is one of two members of the family Chionididae, the other being the snowy sheathbill (*C. alba*), also known as the pale-faced, greater, or wattled sheathbill. The black-faced sheathbill comprises four allopatric subspecies, each confined to an archipelago in the Southern Ocean (Marchant and Higgins, 1993): *C. m. marionensis* (Prince Edward Islands, which somewhat confusingly include Marion Island and Prince Edward Island), *C. m. crozettensis* (Iles Crozet), *C. m. minor* (Iles Kerguelen), and *C. m. nasicornis* (Heard Island). The species is a weak flyer and movement between populations is not known to occur. As the Prince Edward Islands population is the focus of this thesis, all information hereafter will refer specifically to this subspecies.

Black-faced sheathbills (hereafter, sheathbills) are sexually dimorphic (the male is 10% to 15% larger) and form long-term monogamous pair-bonds. Both the Prince Edward Island and Marion Island populations are generally free of predation pressure. Whilst brown skuas (*Catharacta antarctica lonnbergi* Mathews) occasionally pursue sheathbills, kills are infrequent (Burger, 1982) and increasingly so on Marion Island where skuas are rapidly declining (Ryan et al., 2009). Sheathbill survival, lifespan, and the effects of senescence are generally unknown, but the majority of birds begin breeding at four years of age (Burger, 1979) and individuals ringed in the 1970s were still breeding as late as 1995 (Department of Environmental Affairs, unpublished data). Sheathbills breed from November to April. All sheathbill breeding occurs in coastal areas in association with penguins on which they are dependent for breeding (Burger, 1979). The species kleptoparasitizes penguins as they attempt to feed their chicks, and may also prey upon eggs and small chicks (Burger, 1981a). It has been speculated sheathbills would be unable to breed successfully without these high protein sources (Burger, 1981b), though other subspecies are capable of doing so when provided with sufficiently large intertidal zones (Jouventin et al., 1996). The majority of nests are located in structured territories within penguin colonies. Despite a large king penguin

(*Aptenodytes patagonicus* Miller) population on Marion Island, colonies of these birds have relatively few suitable sheathbill nesting sites and the majority of sheathbills breed in rockhopper penguin (*Eudyptes chrysocome filholi* Hutton) colonies (Burger, 1979). Two large macaroni penguin (*Eudyptes chrysolophus* Brandt) colonies are also present but contain the least number of suitable nest sites for sheathbills and exceptional penguin densities limit sheathbill movement within them, rendering these areas of little value to sheathbill breeding (Burger, 1979). Nests are sheltered and up to four eggs are laid. Incubation and fledge periods average 30 and 60 days respectively (Burger, 1979). Nest failure is high and sheathbills appear to have a low breeding rate between 1.07 (Burger 1979) and 0.92 (Huyser *et al.* 2000) fledglings per pair per year.

After the breeding season when the majority of penguins leave the Prince Edward Islands (May to October), sheathbill foraging becomes dependent on the remaining king penguins, the littoral community, and terrestrial macro-invertebrates (Burger, 1978). On Prince Edward Island, sheathbills may forage for invertebrates several km inland (G.T.W. McClelland, personal observation). However, while the Marion Island population formerly foraged far inland as well (Rand, 1954), they now appear limited to coastal areas and are rarely found more than 200 m from the coast (Burger, 1982).

Knowledge of sheathbill demography and breeding biology on the Prince Edward Islands is limited. Though previously studied on Marion Island from 1974-77 (Burger, 1979) and 1994-95 (Huyser et al., 2000), the original 1970s work had sample sizes of six nests or less in two breeding seasons and the 1990s work was limited to a single season. Both studies were limited to a small portion of the eastern side of the island and focused primarily on foraging ecology.

Study Area: The Prince Edward Island group

The sub-Antarctic Prince Edward Island group comprises smaller Prince Edward Island (46°37'S, 37°55'E) and larger Marion Island (46°54'S, 37°45'E) and is located in the Southern Ocean approximately 2300 km southeast of Cape Town, South Africa (Fig. 2). Prince Edward Island receives infrequent human visitation under strict controls while Marion Island is uninhabited aside from a small but continuous presence associated with the meteorological station on the north-east coast. The islands have an oceanic climate (mean annual temperature c. 6.4° C, total precipitation *c*. 2000 mm p.a., 1990s; le Roux and McGeoch,

2008) but are currently experiencing rapid climate change. Mean annual temperature has increased by more than 1° C and precipitation declined by more than 800 mm over the past 50 years (le Roux and McGeoch, 2008).

The Prince Edward Islands are characterised by two biomes; polar desert above 650 m a.s.l., and sub-Antarctic tundra below (Fig. 3; Gremmen and Smith, 2008). Five habitat complexes comprise the sub-Antarctic tundra biome; fellfield (including cushions of *Azorella selago*), biotic (areas manured by seals and seabirds dominated by *Poa cookii* tussock grassland, *Cotulla plumosa* herbfield, and non-native *Poa annua* lawn), saltspray (coastal herbfield of *C. plumosa* and *Crassula moschata*), mire (wet peaty areas consisting of *Agrostis magellanica* grass and bryophytes such as *Sanionia uncinata*, *Blepharidophyllum densifolium*, and *Jamesoniella colorata*), and slope (lowland areas with well-drained slopes dominated by *Blechnum penna-marina* and *Acaena magellanica*).

The islands share most of their indigenous species and are relatively depauparate in plant and invertebrate species richness (Chown and Froneman, 2008). However, they are internationally-important breeding sites for a number of seabirds and seals. Twenty-nine seabird species breed or are suspected to breed between the two islands including four species of penguin, five species of albatross, and 15 species of petrel (Cooper and Brown, 1990; McClelland et al., 2013). Marion Island is especially important for penguins and supports 13 % of the global king penguin population, 80 % of which is divided between two colonies at King Penguin and Kildalkey bays (Crawford and Cooper, 2003). The population of the eastern race of southern rockhopper penguin is 17 % of the world population (Ryan and Bester, 2008). Southern elephant seal (*Mirounga leonine* Linnaeus), Antarctic fur seal (*Arctocephalus gazella* Peters), and 33 % of the global sub-Antarctic fur seal (*Arctocephalus tropicalis* Gray) population are also present on the islands (Hofmeyr et al., 2006). Sheathbills are the lone indigenous terrestrial vertebrate.

Marion Island has far more invasive species than Prince Edward Island (Chown and Froneman, 2008). The now exterminated domestic cat (*Felis catus* Linnaeus) was present on Marion Island from 1949-1991, over which time it was responsible for a significant decline in the Marion Island petrel fauna. Introduced to the island sometime after 1818 (Watkins and Cooper, 1986), house mice continue to persist and forage primarily on terrestrial invertebrates (Smith et al., 2002). Densities are highest in coastal regions (Gleeson, 1981),

but mice have slowly increased their elevational range to have island-wide impacts (Phiri et al., 2008). In consequence of these two vertebrate predators, Prince Edward Island has significantly higher petrel and terrestrial invertebrate densities than Marion Island (Crafford and Scholtz, 1987; Chown et al., 2002). A comprehensive overview of the biology, geology, and climate of the Prince Edward Islands is provided by Chown and Froneman (2008).

Thesis outline

This thesis explores the ecology of an island endemic bird in a changing environment, the black-faced sheathbill on sub-Antarctic Marion Island. The work integrates several disciplines including spatially-explicit capture-mark-recapture modelling, population matrix modelling, and energetics to investigate key questions relating to sheathbills and the Marion Island environment. Each chapter is written and formatted as a stand-alone study with its own aims, methods, results and discussion (Chapters 2-4), whilst Chapter 5 provides a synthesis of the previous chapters and an assessment of the broader topics dealt with in this thesis.

- **Chapter 2** tests empirically whether mouse populations across a range of biologically important habitats on Marion Island have changed through time and whether these changes can be associated significantly with changing abiotic conditions. Changes in invertebrate populations, which have previously been attributed to mouse predation, but with little explicit demographic analysis (see Crafford and Scholtz, 1987; Chown and Smith, 1993; Chown et al., 2002), are also examined to determine whether they can be associated with changing mouse populations, which are shown to remain major predators of invertebrates.
- Insular biotas are remarkably vulnerable to rapid ecosystem change. While many island species declines have been linked to the direct effects of predation or herbivory from invasive species (King, 1985; Donlan et al., 2002; Blackburn et al., 2004), indirect effects are also possible (Lammers and Freeman, 1986; van Riper, 1991; Case, 1996; O'Dowd et al., 2003). Increasingly the threat of global climate change must also be considered. Climate change has the potential to affect island endemics through several pathways including alteration of food webs and in synergy with invasive species (Walther et al., 2002; Zarnetske et al., 2012; Cahill et al., 2013). However, few studies have examined this issue and empirical examples of species responses are lacking. **Chapter 3** addresses such ideas by testing Huyser et al.'s

(2000) hypothesis that sheathbills on Marion Island are in decline due to the combined effects of invasive mice and climate change. The study adopts an integrated approach, examining sheathbill demography, behaviour, and foraging ecology as well as the role of invasive mice, climate change, and penguin declines.

- For basal metabolic rate (BMR), species or groups that are phylogenetically or ecologically distinct often have rates beyond the norm (McNab, 1995, 1996; Bozinovic et al., 2004). Sheathbills are both atypical Charadriiformes (Livezey, 2010) and one of only a few high latitude island endemic birds. **Chapter 4** therefore tests if the phylogenetic position and ecology of sheathbills equate to a unique BMR when allometrically compared to other bird species. Further, as BMR underlies all processes contributing to a species' ecology including behaviour, distribution, and life history (Brown et al., 2004; White et al., 2007; Biro and Stamps, 2010) knowledge of sheathbill metabolism contributes to our understanding how specie persist on islands and how they may be affected by ecosystem change.
- Finally, **Chapter 5** draws together the outcomes of this work and considers the consequences of the observed interactions between climate change, invasive house mice and black-faced sheathbills. Management implications and future work are also addressed.

References

Alcover, J.A., Sans, A., Palmer, M., 1998. The extent of extinctions of mammals on islands. Journal of Biogeography 25, 913–918.

Angel, A., Cooper, J., 2006. A review of the impacts of introduced rodents on the islands of Tristan and Gough. Royal Society for the Protection of Birds, Report No. 17.

Angel, A., Wanless, R.M., Cooper, J., 2008. Review of impacts of the introduced house mouse on islands in the Southern Ocean: are mice equivalent to rats? Biological Invasions 11, 1743–1754.

Atkinson, I.A.E., 1985. The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifaunas, in: Moors, P.J. (Ed.), Conservation of Island Birds. Cambridge: International Council for Bird Preservation Technical Publication No. 3, pp. 35–81.

Baur, G., 1891. On the origin of the Galapagos Islands. American Naturalist 25, 217–229.

Benning, T.L., LaPointe, D., Atkinson, C.T., Vitousek, P.M., 2002. Interactions of climate change with biological invasions and land use in the Hawaiian Islands: modeling the fate

of endemic birds using a geographic information system. Proceedings of the National Academy of Sciences of the U.S.A. 99, 14246–14249.

Bergstrom, D.M., Chown, S.L., 1999. Life at the front: history, ecology and change on Southern Ocean islands. Trends in Ecology and Evolution 14, 472–477.

Bergstrom, D.M., Lucieer, A., Kiefer, K., Wasley, J., Belbin, L., Pedersen, T.K., Chown, S.L., 2009. Indirect effects of invasive species removal devastate World Heritage Island. Journal of Applied Ecology 46, 73–81.

Biber, E., 2002. Patterns of endemic extinctions among island bird species. Ecography 6, 661–676.

Biro, P.A., Stamps, J.A., 2010. Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? Trends in Ecology and Evolution 25, 653–659.

Blackburn, T.M., Cassey, P., Duncan, R.P., Evans, K.L., Gaston, K.J., 2004. Avian extinction and mammalian introductions on oceanic islands. Science 305, 1955–1958.

Blondel, J., 2000. Evolution and ecology of birds on islands: trends and prospects. Vie Et Milieu 50, 205–220.

Bowen, L., Van Vuren, D., 1997. Insular endemic plants lack defenses against herbivores. Conservation Biology 11, 1249–1254.

Bozinovic, F., Ruiz, G., Rosenmann, M., 2004. Energetics and torpor of a South American "living fossil", the microbiotheriid *Dromiciops gliroides*. Journal of Comparative Physiology B 174, 293–297.

Brodier, S., Pisanu, B., Villers, A., Pettex, E., Lioret, M., Chapuis, J.-L., Bretagnolle, V., 2011. Responses of seabirds to the rabbit eradication on Ile Verte, sub-Antarctic Kerguelen Archipelago. Animal Conservation 14, 459–465.

Brook, B.W., 2008. Synergies between climate change, extinctions and invasive invertebrates. Wildlife Research 35, 249–252.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. Ecology 85, 1771–1789.

Burger, A.E., 1978. Terrestrial invertebrates: a food resource for birds at Marion Island. South African Journal of Antarctic Research 8, 87–99.

Burger, A.E., 1979. Breeding biology, moult, and survival of lesser sheathbills *Chionis minor* at Marion Island. Ardea 67, 1–14.

Burger, A.E., 1981a. Food and foraging behaviour of lesser sheathbills at Marion Island. Ardea 69, 167–180.

Burger, A.E., 1981b. Time budgets, energy needs, and kleptoparasitism in breeding lesser sheathbills (*Chionis minor*). Condor 83, 106–112.

Burger, A.E., 1982. Foraging behaviour of lesser sheathbills *Chionis minor* exploiting invertebrates on a Sub-Antarctic island. Oecologia 52, 236–245.

Cahill, A.E., Aiello-Lammens, M.E., Fisher-Reid, M.C., Hua, X., Karanewsky, C.J., Yeong Ryu, H., Sbeglia, G.C., Spagnolo, F., Waldron, J.B., Warsi, O., Wiens, J.J., 2013. How does climate change cause extinction? Proceedings of the Royal Society B 280, doi: 10.1098/rspb.2012.1890.

Cannon, R.J.C., 1998. The implications of predicted climate change for insect pests in the UK, with emphasis on non-indigenous species. Global Change Biology 4, 785–796.

Carlquist, S., 1966. The biota of long-distance dispersal. I. Principles of dispersal and evolution. Quarterly Review of Biology 41, 247–270.

Carlquist, S., 1974. Island biology. Columbia University Press, New York.

Case, T.J., 1996. Global patterns in the establishment and distribution of exotic birds. Biological Conservation 78, 69–96.

Cassey, P., Blackburn, T.M., 2004. Body size trends in a Holocene island bird assemblage. Ecography 27, 59–68.

Chen, A.X., He, F., 2009. Speciation and endemism under the model of island biogeography. Ecology 90, 39–45.

Chown, S.L., Convey, P., 2007. Spatial and temporal variability across life's hierarchies in the terrestrial Antarctic. Philosophical Transactions of the Royal Society B 362, 2307–2331.

Chown, S.L., Froneman, P.W., 2008. The Prince Edward Islands: land-sea interactions in a changing ecosystem. Sun Press, Stellenbosch.

Chown, S.L., McGeoch, M.A., Marshall, D.J., 2002. Diversity and conservation of invertebrates on the sub-Antarctic Prince Edward Islands. African Entomology 10, 67–82.

Chown, S.L., Slabber, S., McGeoch, M.A., Janion, C., Leinaas, H.P., 2007. Phenotypic plasticity mediates climate change responses among invasive and indigenous arthropods. Proceedings of the Royal Society B 274, 2531–2537.

Chown, S.L., Smith, V.R., 1993. Climate change and the short-term impact of feral house mice at the sub-Antarctic Prince Edward Islands. Oecologia 96, 508–516.

Clegg, S., 2009. Evolutionary changes following island colonization in birds, in: Losos, J.B., Ricklefs, R.E. (Eds.), Theory of Island Biogeography Revisited. Princeton University Press, Princeton, pp. 293–324.

Clegg, S.M., Owens, I.P.F., 2002. The “island rule” in birds: medium body size and its ecological explanation. Proceedings of the Royal Society B 269, 1359–1365.

Coblentz, B.E., 1978. The effects of feral goats (*Capra hircus*) on island ecosystems. Biological Conservation 13, 279–286.

Cody, M.L., McC. Overton, J., 1996. Short-term evolution of reduced dispersal in island plant populations. Journal of Ecology 84, 53–61.

Convey, P., 2006. Antarctic climate change and its influences on terrestrial ecosystems, in: Bergstrom, D.M., Convey, P., Huiskes, A.H.L. (Eds.), Trends in Antarctic Terrestrial and Limnetic Ecosystems. Springer, Dordrecht, pp. 253–272.

Convey, P., 2010. Terrestrial biodiversity in Antarctica – Recent advances and future challenges. Polar Science 4, 135–147.

Cook, A.J., Poncet, S., Cooper, A.P.R., Herbert, D.J., Christie, D., 2010. Glacier retreat on South Georgia and implications for the spread of rats. Antarctic Science 22, 255–263.

Cooper, J., Brown, C.R., 1990. Ornithological research at the sub-Antarctic Prince Edward Islands: a review of achievements. South African Journal of Antarctic Research 20, 40–57.

Courchamp, F., Chapuis, J., Pascal, M., 2003. Mammal invaders on islands: impact, control and control impact. Biological Reviews 78, 347–383.

Covas, R., 2012. Evolution of reproductive life histories in island birds worldwide. Proceedings of the Royal Society B 279, 1531–1537.

Cox, G.W., Ricklefs, R.E., 1977. Species diversity and ecological release in Caribbean land bird faunas. Oikos 28, 113–122.

Cox, P.M., Betts, R.A., Jones, C.D., Spall, S.A., Totterdell, I.J., 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature 408, 184–187.

Crafford, J.E., 1990. The role of feral house mice in ecosystem functioning on Marion Island, in: Kerry, K., Hempel, G. (Eds.), Antarctic Ecosystems: Ecological Change and Conservation. Springer-Verlag, Berlin, pp. 359–364.

Crafford, J.E., Scholtz, C.H., 1987. Quantitative differences between the insect faunas of Sub-Antarctic Marion and Prince Edward Islands: a result of human intervention? Biological Conservation 40, 255–262.

Crafford, J.E., Scholtz, C.H., Chown, S.L., 1986. The insects of sub-Antarctic Marion and Prince Edward Islands; with a bibliography of entomology of the Kerguelen Biogeographical Province. South African Journal of Antarctic Research 16, 41–84.

Crawford, R.J.M., Cooper, J., 2003. Conserving surface-nesting seabirds at the Prince Edward Islands: the role of research, monitoring, and legislation. African Journal of Marine Science 25, 415–426.

Cronk, Q.C.B., 1997. Islands: stability, diversity, conservation. Biodiversity and Conservation 6, 477–493.

Curnutt, J., Pimm, S.L., 2001. How many bird species in Hawaii and the Central Pacific before first contact? Studies in Avian Biology 22, 15–30.

Cuthbert, R., Hilton, G., 2004. Introduced house mice *Mus musculus*: a significant predator of threatened and endemic birds on Gough island, South Atlantic Ocean. Biological Conservation 117, 483–489.

Darlington, P.J., 1943. Carabidae of mountains and islands: data on the evolution of isolated faunas, and on atrophy of wings. Ecological Monographs 13, 37–61.

Darwin, C., 1859. On the origin of species, 1st ed. John Murray, London.

Dayan, T., Simberloff, D., 2005. Ecological and community-wide character displacement: the next generation. Ecology Letters 8, 875–894.

Delgado García, J.D., 2002. Interaction between introduced rats and a frugivore bird-plant system in a relict island forest. Journal of Natural History 36, 1247–1258.

Denno, R.F., Hawthorne, D.J., Thorne, B.L., Gratton, C., 2001. Reduced flight capapbility in British Virgin Island populations of a wing-dimorphic insect: the role of habitat isolation, persistence, and structure. Ecological Entomology 26, 25–36.

Donlan, C.J., Tershy, B.R., Croll, D.A., 2002. Islands and introduced herbivores: conservation action as ecosystem experimentation. Journal of Applied Ecology 39, 235–246.

Dukes, J.S., Mooney, H.A., 1999. Does global change increase the success of biological invaders? Trends in Ecology and Evolution 14, 135–139.

Duncan, R.P., Blackburn, T.M., 2004. Extinction and endemism in the New Zealand avifauna. Global Ecology and Biogeography 13, 509–517.

Duncan, R.P., Blackburn, T.M., 2007. Causes of extinction in island birds. Animal Conservation 10, 149–150.

Duncan, R.P., Boyer, A.G., Blackburn, T.M., 2013. Magnitude and variation of prehistoric bird extinctions in the Pacific. Proceedings of the National Academy of Sciences of the U.S.A. 110, 6436–6441.

Frankham, R., 1995. Conservation genetics. Annual Review of Genetics 29, 305–327.

Frenot, Y., Chown, S.L., Whinam, J., Selkirk, P.M., Convey, P., Skotnicki, M., Bergstrom, D.M., 2005. Biological invasions in the Antarctic: extent, impacts and implications. Biological Reviews 80, 45–72.

Gill, F., Wright, M., 2006. Birds of the world: recommended English names. Princeton University Press, Princeton.

Gleeson, J.P., 1981. Ecology of the house mouse *Mus musculus* Linnaeus, on Marion Island. MSc. thesis, University of Pretoria, South Africa.

Grant, P.R., 1965. The adaptive significance of some size trends in island birds. Evolution 19, 355–367.

Grant, P.R., 1998. Evolution on islands. Oxford University Press, Oxford.

Gremmen, N.J.M., Smith, V.R., 2008. Terrestrial vegetation and dynamics, in: Chown, S.L., Froneman, P.W. (Eds.), The Prince Edward Islands: Land-sea Interactions in a Changing Ecosystem. Sun Press, Stellenbosch, pp. 215–244.

Gressitt, B.J.L., Weber, N.A., 1959. Bibliographic introduction to Antarctic-Subantarctic entomology. Pacific Insects 1, 441–480.

Gressitt, J.L., 1970. Subantarctic entomology and biogeography. Pacific Insects Monographs 23, 295–374.

Hansen, D.M., Olesen, J.M., Jones, C.G., 2002. Trees , birds and bees in Mauritius: exploitative competition between introduced honey bees and endemic nectarivorous birds? Journal of Biogeography 29, 721–734.

Hansen, J., Sato, M., Ruedy, R., 2012. Perception of climate change. Proceedings of the National Academy of Sciences of the U.S.A. 109, E2415–E2423.

Harris, D.B., Macdonald, D.W., 2007. Interference competition between introduced black rats and endemic Galapagos rice rats. Ecology 88, 2330–2344.

Hellmann, J.J., Byers, J.E., Bierwagen, B.G., Dukes, J.S., 2008. Five potential consequences of climate change for invasive species. Conservation Biology 22, 534–543.

Hofmeyr, G.J.G., Bester, M.N., Makhado, A.B., Pistorius, P.A., 2006. Population changes in Subantarctic and Antarctic fur seals at Marion Island. South African Journal of Wildlife Research 36, 55–68.

Holdaway, R.N., 1999. Introduced predators and avifaunal extinction in New Zealand, in: McPhee, R.D. (Ed.), Extinctions in Near Time. Kluwer Academic/Plenum, New York, pp. 189–238.

Honegger, R.E., 1981. List of amphibians and reptiles either known or thought to have become extinct since 1600. Biological Conservation 19, 141–158.

Huyser, O., Ryan, P.G., Cooper, J., 2000. Changes in population size, habitat use and breeding biology of lesser sheathbills (*Chionis minor*) at Marion Island: impacts of cats, mice and climate change? Biological Conservation 92, 299–310.

Imber, M.J., Bell, B.D., Bell, E.A., 2005. Antipodes Islands birds in autumn 2001. Notornis 52, 125–132.

Ingram, J.C., Dawson, T.P., 2005. Climate change impacts and vegetation response on the island of Madagascar. Proceedings of the Royal Society A 363, 55–59.

Janion, C., Leinaas, H.P., Terblanche, J.S., Chown, S.L., 2010. Trait means and reaction norms: the consequences of climate change/invasion interactions at the organism level. Evolutionary Ecology 24, 1365–1380.

Johnson, K.P., Adler, F.R., Cherry, J.L., 2000. Genetic and phylogenetic consequences of island biogeography. Evolution 54, 387–396.

Johnson, T.H., Stattersfield, A.J., 1990. A global review of island endemic birds. Ibis 132, 167–180.

Jones, A.G., Chown, S.L., Gaston, K.J., 2003. Introduced house mice as a conservation concern on Gough Island. Biodiversity and Conservation 12, 2107–2119.

Jones, A.G., Chown, S.L., Ryan, P.G., Gremmen, N.J.M., Gaston, K.J., 2003. A review of conservation threats on Gough Island: a case study for terrestrial conservation in the Southern Oceans. Biological Conservation 113, 75–87.

Jones, H.P., Tershy, B.R., Zavaleta, E.S., Croll, D.A., Keitt, B.S., Finkelstein, M.E., Howald, G.R., 2008. Severity of the effects of invasive rats on seabirds: a global review. Conservation Biology 22, 16–26.

Jouventin, P., Bried, J., Ausilio, E., 1996. Life-history variations of the lesser sheathbill *Chionis minor* in contrasting habitats. Ibis 138, 732–741.

Kalmar, A., Currie, D.J., 2006. A global model of island biogeography. Global Ecology and Biogeography 15, 72–81.

Kalmar, A., Currie, D.J., 2007. A unified model of avian species richness on islands and continents. Ecology 88, 1309–1321.

Kier, G., Kreft, H., Lee, T.M., Jetz, W., Ibisch, P.L., Nowicki, C., Mutke, J., Barthlott, W., 2009. A global assessment of endemism and species richness across island and mainland regions. Proceedings of the National Academy of Sciences of the U.S.A. 106, 9322–9327.

King, W.B., 1985. Island birds: will the future repeat the past?, in: Conservation of Island Birds. ICBP Technical Publication No. 3, pp. 3–15.

Kreft, H., Jetz, W., Mutke, J., Kier, G., Barthlott, W., 2008. Global diversity of island floras from a macroecological perspective. Ecology Letters 11, 116–127.

Kurle, C.M., Croll, D.A., Tershy, B.R., 2008. Introduced rats indirectly change marine rocky intertidal communities from algae- to invertebrate-dominated. Proceedings of the National Academy of Sciences of the U.S.A. 105, 3800–3804.

Lack, D., Southern, H.N., 1949. Birds on Tenerife. Ibis 91, 607–626.

Lammers, T.G., Freeman, C.E., 1986. Ornithophily among the Hawaiian Lobelioideae (Campanulaceae): evidence from floral nectar sugar compositions. American Journal of Botany 73, 1613–1619.

Lebouvier, M., Laparie, M., Hullé, M., Marais, A., Cozic, Y., Lalouette, L., Vernon, P., Candresse, T., Frenot, Y., Renault, D., 2011. The significance of the sub-Antarctic Kerguelen Islands for the assessment of the vulnerability of native communities to climate change, alien insect invasions and plant viruses. Biological Invasions 13, 1195–1208.

Lee, J.E., Slabber, S., Jansen van Vuuren, B., Noort, S., Chown, S.L., 2007. Colonisation of sub-Antarctic Marion Island by a non-indigenous aphid parasitoid *Aphidius matricariae* (Hymenoptera, Braconidae). Polar Biology 30, 1195–1201.

Livezey, B.C., 2010. Phylogenetics of modern shorebirds (Charadriiformes) based on phenotypic evidence: analysis and discussion. Zoological Journal of the Linnean Society 160, 567–618.

Lomolino, M. V, 2005. Body size evolution in insular vertebrates: generality of the island rule. Journal of Biogeography 32, 1683–1699.

Lorvelec, O., Pascal, M., 2005. French attempts to eradicate non-indigenous mammals and their consequences for native biota. Biological Invasions 7, 135–140.

Losos, J.B., Ricklefs, R.E., 2009. Adaptation and diversification on islands. Nature 457, 830–836.

Losos, J.B., Schluter, D., 2000. Analysis of an evolutionary species-area relationship. Nature 408, 847–850.

MacArthur, R.H.W., Wilson, E.O., 1967. The theory of island biogeography. Princeton University Press, Princeton.

Marchant, S., Higgins, P.J., 1993. Handbook of Australian, New Zealand, and Antarctic birds, Vol. 2: Raptors to Lapwings. Oxford University Press, Melbourne.

McClelland, G.T.W., Cooper, J., Chown, S.L., 2013. Evidence of breeding by diving petrels and storm petrels at Marion Island after the eradication of feral cats. Ornithological Observations 4, 90–93.

McNab, B.K., 1994. Resource use and the survival of land and freshwater vertebrates on oceanic islands. American Naturalist 144, 643–660.

McNab, B.K., 1995. Energy expenditure and conservation in frugivorous and mixed-diet carnivorans. Journal of Mammalogy 76, 206–222.

McNab, B.K., 1996. Metabolism and temperature regulation of kiwis (Apterygidae). Auk 113, 687–692.

McNab, B.K., Ellis, H.I., 2006. Flightless rails endemic to islands have lower energy expenditures and clutch sizes than flighted rails on islands and continents. Comparative Biochemistry and Physiology A 145, 295–311.

Meiri, S., Cooper, N., Purvis, A., 2008. The island rule: made to be broken? Proceedings of the Royal Society B 275, 141–148.

Milberg, P., Tyrberg, T., 1993. Naive birds and noble savages - a review of man-caused prehistoric extinctions of island birds. Ecography 16, 229–250.

Miskelly, C.M., Walker, K.J., Elliott, G.P., 2006. Breeding ecology of three Subantarctic snipes (genus *Coenocorypha*). Notornis 53, 361–374.

Morin, M., Conant, S., 1998. Laysan Island ecosystem restoration plan. Unpublished report for the U.S. Fish and Wildlife Service. University of Hawaii at Manoa, Honolulu.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

O'Dowd, D.J., Green, P.T., Lake, P.S., 2003. Invasional "meltdown" on an oceanic island. Ecology Letters 6, 812–817.

Olson, S.L., James, H.F., 1982. Fossil birds from the Hawaiian Islands: evidence for wholesale extinction by man before western contact. Science 217, 633–635.

Phiri, E.E., McGeoch, M.A., Chown, S.L., 2008. Spatial variation in structural damage to a keystone plant species in the sub-Antarctic: interactions between *Azorella selago* and invasive house mice. Antarctic Science 21, 189–196.

Pimm, S., Raven, P., Peterson, A., S, H., 2006. Human impacts on the rates of recent, present, and future bird extinctions. Proceedings of the National Academy of Sciences of the U.S.A. 103, 10941–10946.

Rand, R.W., 1954. Notes on the birds of Marion Island. Ibis 96, 173–206.

Ricklefs, R.E., Lovette, I.J., 1999. The roles of island area *per se* and habitat diversity in the species-area relationships of four Lesser Antillean faunal groups. Journal of Animal Ecology 68, 1142–1160.

Rignot, E., Kanagaratnam, P., 2006. Changes in the velocity structure of the Greenland Ice Sheet. Science 311, 986–990.

Van Riper, C.I., 1991. The impact of introduced vectors and avian malaria on insular passeriform bird populations in Hawaii. Bulletin of the Society for Vector Ecology 16, 59–83.

Robertson, A.W., Kelly, D., Ladley, J.J., Sparrow, A.D., 1999. Effects of pollinator loss on endemic New Zealand mistletoes (Loranthaceae). Conservation Biology 13, 499–508.

Roff, D.A., 1990. The evolution of flightlessness in insects. Ecological Monographs 60, 389–421.

Roff, D.A., 1994. The evolution of flightlessness: is history important? Evolutionary Ecology 8, 639–657.

Roughgarden, J., 1972. Evolution of niche width. American Naturalist 106, 683–718.

le Roux, P.C., McGeoch, M.A., 2008. Changes in climate extremes, variability and signature on sub-Antarctic Marion Island. Climatic Change 86, 309–329.

le Roux, P.C., Ramaswiela, T., Kalwij, J.M., Shaw, J.D., Ryan, P.G., Treasure, A.M., McClelland, G.T.W., McGeoch, M.A., Chown, S.L., 2013. Human activities, propagule pressure and alien plants in the sub-Antarctic: Tests of generalities and evidence in support of management. Biological Conservation 161, 18–27.

Rowe-Rowe, D.T., Green, B., Crafford, J.E., 1989. Estimated impact of feral house mice on Sub-Antarctic invertebrates at Marion Island. Polar Biology 9, 457–460.

Ruffino, L., Bourgeois, K., Vidal, E., Icard, J., Torre, F., Legrand, J., 2008. Introduced predators and cavity-nesting seabirds: unexpected low level of interaction at breeding sites. Canadian Journal of Zoology 86, 1068–1073.

Russell, J.C., 2011. Indirect effects of introduced predators on seabird islands, in: Mulder, C.P.H., Anderson, W.B., Towns, D.R., Bellingham, P.J. (Eds.), Seabird Islands: Ecology, Invasion, and Restoration. Oxford University Press, New York, pp. 261–279.

Ryan, P.G., Bester, M.N., 2008. Pelagic predators, in: Chown, S.L., Froneman, P.W. (Eds.), The Prince Edward Islands: Land-sea Interactions in a Changing Ecosystem. Sun Press, Stellenbosch, pp. 121–164.

Ryan, P.G., Whittington, P.A., Crawford, R.J.M., 2009. A tale of two islands: contrasting fortunes for Subantarctic skuas at the Prince Edward Islands. African Journal of Marine Science 31, 431–437.

Sadler, J.P., 1996. Biodiversity on oceanic islands: a palaeoecological assessment. Journal of Biogeography 26, 75–87.

Savidge, J.A., 1987. Extinction of an island forest avifauna by an introduced snake. Ecology 68, 660–668.

Schermann-Legionnet, A., Hennion, F., Vernon, P., Atlan, A., 2007. Breeding system of the subantarctic plant species *Pringlea antiscorbutica* R. Br. and search for potential insect pollinators in the Kerguelen Islands. Polar Biology 30, 1183–1193.

Schluter, D., 1988. The evolution of finch communities on islands and continents: Kenya vs. Galapagos. Ecological Monographs 58, 229–249.

Schluter, D., 2000. The ecology of adaptive radiation. Oxford University Press, Oxford.

Schoener, T.W., Spiller, D.A., 1996. Devastation of prey diversity by experimentally introduced predators in the field. Nature 381, 691–694.

Schoener, T.W., Spiller, D.A., 1999. Indirect effects in an experimentally staged invasion by a major predator. American Naturalist 153, 347–358.

Scott, S.N., Clegg, S.M., Blomberg, S.P., Kikkawa, J., Owens, I.P.F., 2003. Morphological shift in island-dwelling birds: the roles of generalist foraging and niche expansion. Evolution 57, 2147–2156.

Simberloff, D., 1994. The ecology of extinction. Acta Palaeontologica Polonica 38, 159–174.

Simberloff, D., 2009. Rats are not the only introduced rodents producing ecosystem impacts on islands. Biological Invasions 11, 1735–1742.

Smith, V.R., Avenant, N.L., Chown, S.L., 2002. The diet and impact of house mice on a sub-Antarctic island. Polar Biology 25, 703–715.

Smith, V.R., Steenkamp, M., 1990. Climatic change and its ecological implications at a Subantarctic island. Oecologia 85, 14–24.

Sorte, C.J.B., Ibáñez, I., Blumenthal, D.M., Molinari, N.A., Miller, L.P., Grosholz, E.D., Diez, J.M., D'Antonio, C.M., Olden, J.D., Jones, S.J., Dukes, J.S., 2013. Poised to prosper? A cross-system comparison of climate change effects on native and non-native species performance. Ecology Letters 16, 261–270.

Stachowicz, J.J., Terwin, J.R., Whitlatch, R.B., Osman, R.W., 2002. Linking climate change and biological invasions: Ocean warming facilitates nonindigenous species invasions. Proceedings of the National Academy of Sciences of the U.S.A. 99, 15497–15500.

Steadman, D.W., 1995. Prehistoric extinctions of Pacific island birds: biodiversity meets zooarchaeology. Science 267, 1123–1131.

Steadman, D.W., 2006. Extinction and biogeography of tropical Pacific birds. Chicago University Press, Chicago.

Stuart, Y.E., Losos, J.B., Algar, A.C., B, P.R.S., 2012. The island − mainland species turnover relationship. Proceedings of the Royal Society B 279, 4071–4077.

Svanbäck, R., Bolnick, D.I., 2007. Intraspecific competition drives increased resource use diversity within a natural population. Proceedings of the Royal Society B 274, 839–844.

Szabo, J.K., Khwaja, N., Garnett, S.T., Butchart, S.H.M., 2012. Global patterns and drivers of avian extinctions at the species and subspecies level. PloS one 7, e47080.

Terborgh, J., 2009. The trophic cascades on islands, in: Losos, J.B., Ricklefs, R.E. (Eds.), Theory of Island Biogeography Revisited. Princeton University Press, Princeton, pp. 116–142.

Thost, D., Allison, I., 2006. The climate of Heard Island, in: Green, K., Woehler, E. (Eds.), Heard Island: Southern Ocean Sentinel. Surrey, Beatty and Sons, Chipping Norton, Australia, pp. 52–68.

Towns, D.R., Atkinson, I.A.E., Daugherty, C.H., 2006. Have the harmful effects of introduced rats on islands been exaggerated? Biological Invasions 8, 863–891.

Towns, D.R., Broome, K.G., 2003. From small Maria to massive Campbell: forty years of rat eradications from New Zealand islands. New Zealand Journal of Zoology 30, 377–398.

Tylianakis, J.M., Didham, R.K., Bascompte, J., Wardle, D.A., 2008. Global change and species interactions in terrestrial ecosystems. Ecology Letters 11, 1351–1363.

Van Valen, L.M., 1965. Morphological variation and width of ecological niche. American Naturalist 99, 377–390.

Van Valen, L.M., 1973. A new evolutionary law. Evolutionary Theory 1, 1–30.

Vié, J.-C., Hilton-Taylor, C., Stuart, S.N., 2008. Wildlife in a changing world: an analysis of the 2008 IUCN Red List of Threatened Species. IUCN, Gland, Switzerland.

Wallace, A.R., 1881. Island life: or, the phenomena and causes of insular faunas and floras, including a revision and attempted solution of the problem of geological climates. Harper, London.

Walther, G., Post, E., Convey, P., Menzel, A., Parmesank, C., Beebee, T.J.C., Fromentin, J., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. Nature 416, 389–395.

Walther, G., Roques, A., Hulme, P.E., Sykes, M.T., Pysek, P., Kühn, I., Zobel, M., Bacher, S., Botta-Dukát, Z., Bugmann, H., Czúcz, B., Dauber, J., Hickler, T., Jarosík, V., Kenis, M., Klotz, S., Minchin, D., Moora, M., Nentwig, W., Ott, J., Panov, V.E., Reineking, B., Robinet, C., Semenchenko, V., Solarz, W., Thuiller, W., Vilà, M., Vohland, K., Settele, J., 2009. Alien species in a warmer world: risks and opportunities. Evolution 24, 686–693.

Wanless, R.M., Angel, A., Cuthbert, R.J., Hilton, G.M., Ryan, P.G., 2007. Can predation by invasive mice drive seabird extinctions? Biology Letters 3, 241–244.

Wanless, R.M., Ratcliffe, N., Angel, A., Bowie, B.C., Cita, K., Hilton, G.M., Kritzinger, P., Ryan, P.G., Slabber, M., 2012. Predation of Atlantic petrel chicks by house mice on Gough Island. Animal Conservation 15, 472–479.

Wanless, R.M., Ryan, P.G., Altwegg, R., Angel, A., Cooper, J., Cuthbert, R., Hilton, G.M., 2009. From both sides: dire demographic consequences of carnivorous mice and longlining for the Critically Endangered Tristan albatrosses on Gough Island. Biological Conservation 142, 1710–1718.

Watkins, B.P., Cooper, J., 1986. Introduction, present status and control of alien species at the Prince Edward Islands, sub-Antarctic. South African Journal of Antarctic Research 16, 86–94.

White, C.R., Cassey, P., Blackburn, T.M., 2007. Allometric exponents do not support a universal metabolic allometry. Ecology 88, 315–323.

White, E.M., Wilson, J.C., Clarke, A.R., 2006. Biotic indirect effects: a neglected concept in invasion biology. Diversity and Distributions 12, 443–455.

Whittaker, R.J., Fernández-Palacios, J.M., 2007. Island biogeography. Ecology, evolution and conservation. Oxford University Press, Oxford, UK.

Whittaker, R.J., Triantis, K.A., Ladle, R.J., 2008. A general dynamic theory of oceanic island biogeography. Journal of Biogeography 35, 977–994.

Williamson, M., Goodhart, C.B., Webb, D.A., Cohen, J., 1989. Natural extinction on islands. Proceedings of the Royal Society B 325, 457–468.

Yoder, J.B., Clancey, E., Des Roches, S., Eastman, J.M., Gentry, L., Godsoe, W., Hagey, T.J., Jochimsen, D., Oswald, B.P., Robertson, J., Sarver, B.A.J., Schenk, J.J., Spear, S.F., Harmon, L.J., 2010. Ecological opportunity and the origin of adaptive radiations. Journal of Experimental Biology 23, 1581–1596.

Zarnetske, P.L., Skelly, D.K., Urban, M.C., 2012. Biotic multipliers of climate change. Science 336, 1516–1518.

Figure Legends

Figure 1: A) Adult black-faced sheathbill (*Chionis minor marionensis*; Marion Island), B) sheathbill with a hand-held GPS and field book (Marion Island), C) adult sheathbill kleptoparasitizing a king penguin (*Aptenodytes patagonicus;* Marion Island) as it attempts to feed its chick, D) a flock of sheathbills foraging for terrestrial invertebrates (Prince Edward Island), E) two sheathbills scavenge a king penguin carcass (Marion Island), F) sheathbill breeding pair with a rockhopper penguin (*Eudyptes chrysocome filholi*; Marion Island), G) sheathbill with nestling at nest site (Marion Island), H) researcher monitoring a sheathbill nest in a rockhopper penguin colony (Marion Island).

Figure 2: Location of the Prince Edward Islands and other islands in which black-faced sheathbills occur.

Figure 3: The six habitat complexes on the Prince Edward Islands as identified by Gremmen and Smith (2008), namely A) polar desert, B) fellfield, C) biotic, D) saltspray, E) mire, F) slope.

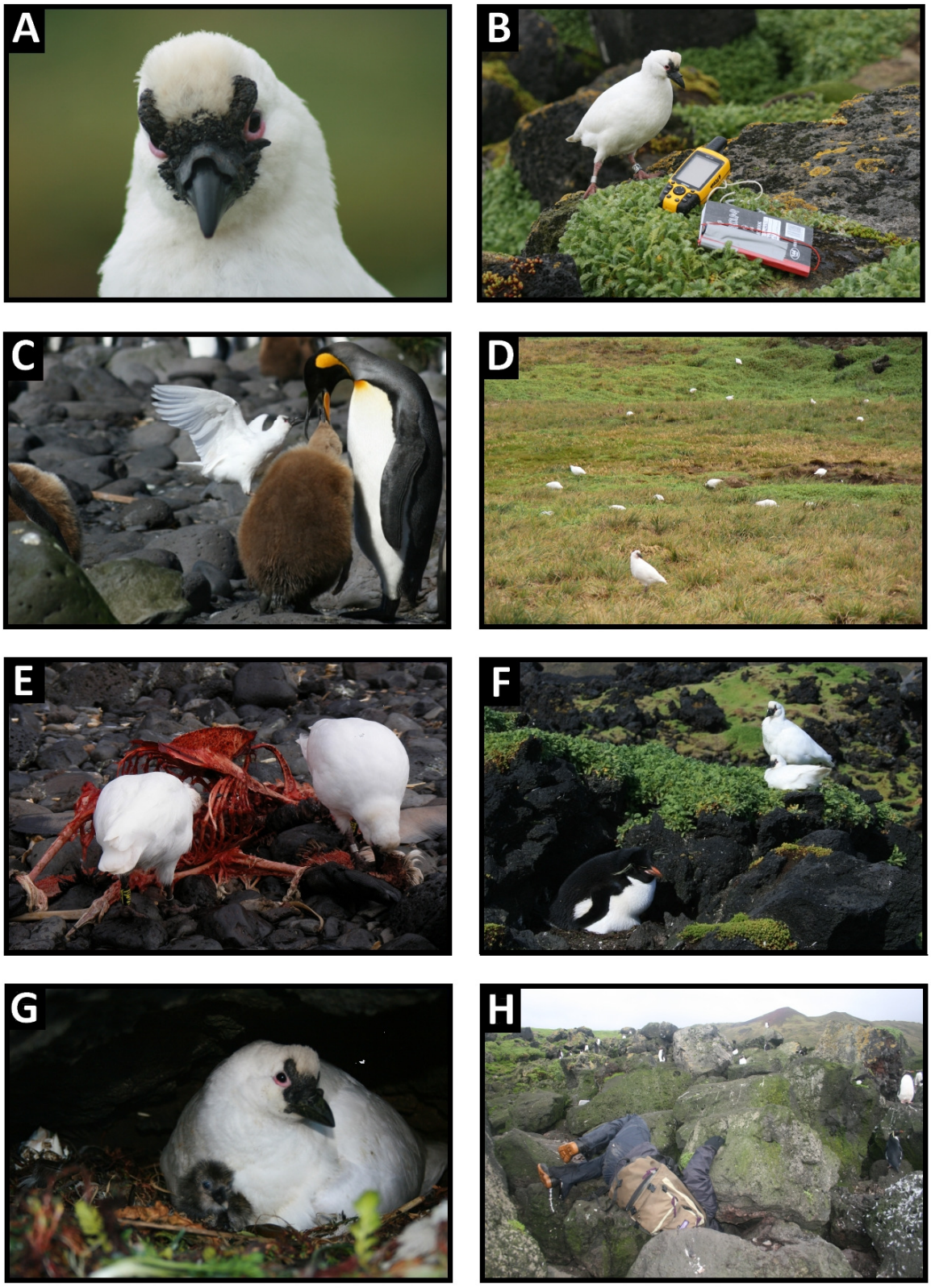


Figure 1

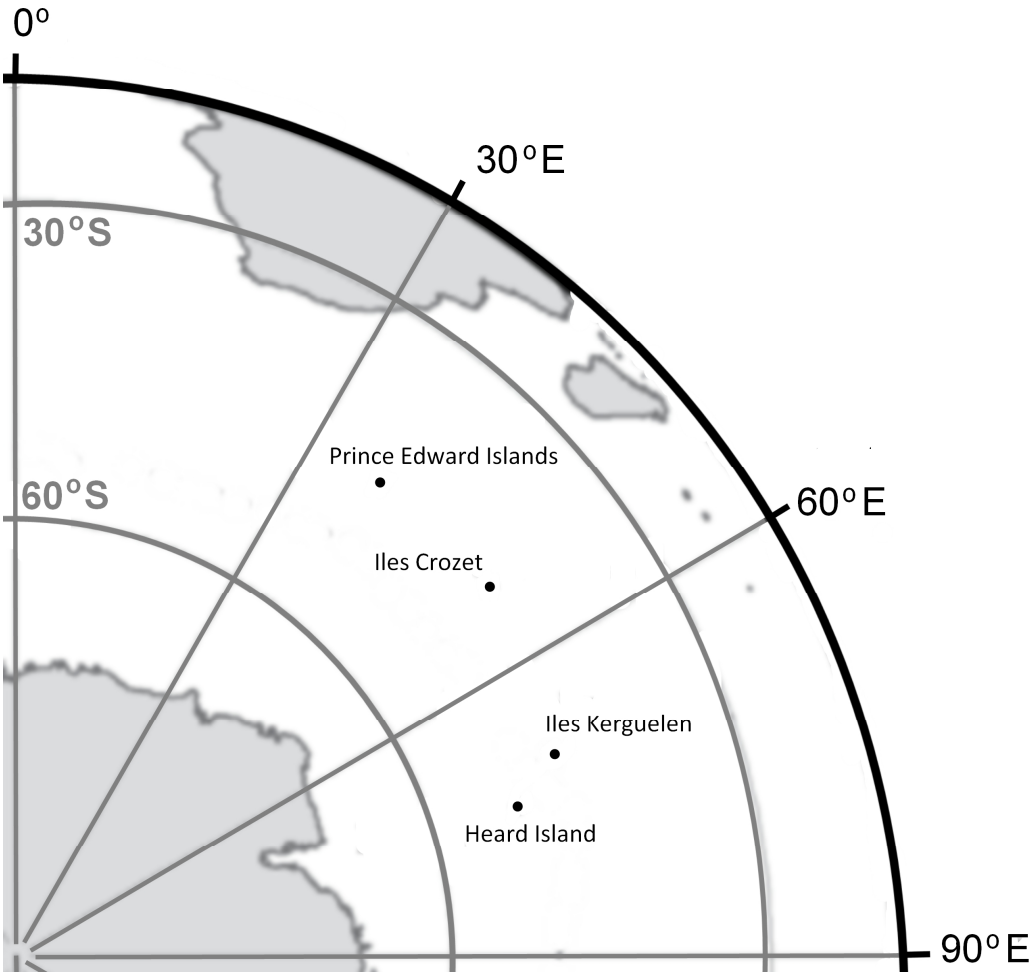


Figure 2

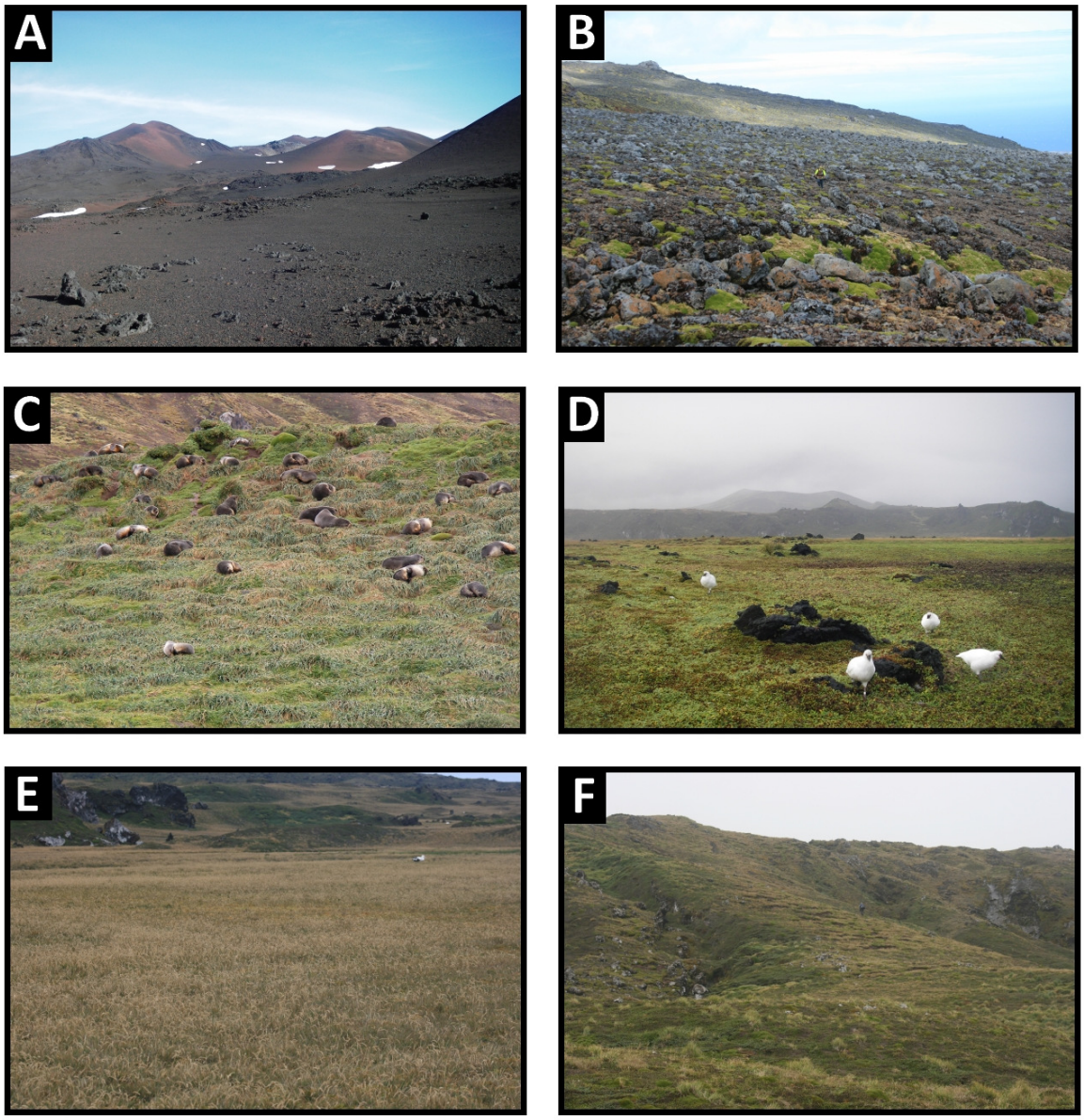


Figure 3

Chapter 2: Climate change-mediated increases in an invasive rodent and its impact on endemic invertebrates on a Southern Ocean island.

"I saw a hole with ears of grass dragged into it, and like a mouse's. It is not unlikely that there is a mouse in the island" **– H.N. Mosely, Marion Island, 1879**

A young house mouse (*Mus musculus*) receives an ear tag on Marion Island. Photograph by Ryan Reissinger

Introduction

Islands are home to some of the world's most remarkable species. These range from dwarf mammals to many species of flightless birds and insects (Carlquist, 1974). Island biotas have also proven exceptionally important in the development of ecological and evolutionary thought (Darwin, 1859; Wallace, 1881; MacArthur and Wilson, 1967; Losos et al., 1998; Ricklefs and Lovette, 1999). However, owing to a combination of endemicity, isolation and in some cases local geography, island biodiversity has also proven remarkably sensitive to anthropogenic disturbance (Milberg and Tyrberg, 1993; Paulay, 1994; Steadman, 1995; Whittaker and Fernández-Palacios, 2007; Loehle and Eschenbach, 2012; Walsh et al., 2012), at times to the detriment of the humans that have colonized them (Anderson, 2002; Diamond, 2007).

Alongside direct habitat alteration on inhabited islands, biological invasions pose one of the most significant threats to island biodiversity. They have resulted in the extinction of many species (King, 1985; Courchamp et al., 2003; Blackburn et al., 2004), are posing substantive threats to others (McGeoch et al., 2010; Walsh et al., 2012), and have led to the wholesale transformation of entire ecosystems, including as a consequence of control efforts (Vitousek et al., 1997; Zavaleta et al., 2001; Bergstrom et al., 2009). As the pace of climate change has begun to accelerate (Cox et al., 2000; Hansen et al., 2006; Rignot and Kanagaratnam, 2006) so too has it become clear that the direct impacts thereof are likely to have profound consequences for many island systems (Bergstrom and Chown, 1999; Benning et al., 2002; Ingram and Dawson, 2005). Moreover, it has also been suggested that climate change will exacerbate the effects of many invasive species, so further impacting both diversity and ecosystem functioning (Dukes and Mooney, 1999; Chown and Convey, 2007; Walther et al., 2009). These impacts are thought to be most significant for islands that are largely free of permanent human inhabitants.

The most significant invasive animal species on such islands are predators. The role of larger carnivores (such as cats and foxes) is widely recognized (King, 1985; Bailey, 1993; Blackburn et al., 2004; Medina et al., 2011), and in many cases eradication programmes have been undertaken successfully (Bester et al., 2000; Ebbert and Byrd, 2000; Veitch, 2001; Nogales et al., 2004). However, rodents are perhaps just as significant. At least 90% of the

world's islands have been colonized by human commensal rodent species (Atkinson, 1985), including most of the world's largely uninhabited islands (Atkinson, 1985; Frenot et al., 2005; Major et al., 2006). These have been responsible for large population declines of seabirds, invertebrates and plants (Atkinson, 1985; King, 1985; Jones et al., 2008; Athens, 2009; St Clair, 2011). Even species such as house mice (*Mus musculus* Linnaeus), initially thought unable to impact larger prey, pose a considerable conservation threat to seabirds, including species as large as the Tristan albatross (*Diomedea dabbenena* Mathews; Angel and Cooper, 2006; Wanless et al., 2009, 2012). Rodents have also been shown to have considerable indirect effects on ecosystem functioning (Fukami et al., 2006; Wardle et al., 2007; Kurle et al., 2008; Mulder et al., 2008).

Several predictions have been made that these considerable impacts of rodents are likely to be compounded by climate change, especially in more temperate ecosystems. Here, rodents may be constrained by an interaction between severe climates and food limitation (Delong, 1967; Berry, 1968; Berry et al., 1979). Climate change is likely to influence both thermal and resource restrictions on rodents. Given the relationship between temperature and development rate in ectotherms, warming temperatures have the potential to increase prey populations by alleviating the thermal constraints of development and reproduction for many invertebrate species (Honêk, 1996; Bale et al., 2002; Deutsch et al., 2008). In a similar manner, increases in prey resources in addition to ameliorating temperatures are likely to enhance rodent survival, depress the metabolic costs of thermoregulation, and allow rodents to divert more resources to reproduction (Singleton et al., 2005; Bronson, 2009). In turn, it is expected that rodents may be capable of substantially depressing the populations of favoured prey species.

Forecasts for such interactions have been most pronounced for the Southern Ocean islands (Kennedy, 1995; Bergstrom and Chown, 1999; Le Roux et al., 2002; Smith, 2002; Frenot et al., 2005; Convey, 2011), which are home to a wide variety of endemic species including many IUCN listed seabirds and which are considered internationally significant conservation areas (Chown et al., 2001). Indeed, it has been argued that rodents pose the most significant current and future threats to conservation in the region. However, firm evidence for changing rodent populations that are, at the very least, significantly correlated, in the expected direction, with climate change, and demonstrations of associated

relationships with prey populations are entirely absent for the region. Whilst inferences have been drawn from short-term data (Chown and Smith, 1993; van Aarde et al., 1996), population-based assessments are missing. Given this situation and the conservation significance of these islands (Bergstrom and Chown, 1999; Broome, 2009; Convey, 2010) here I test directly these ideas using long-term datasets on the populations of mice and their invertebrate prey from sub-Antarctic Marion island. In particular, I determine whether mouse populations across a range of significant habitats have changed through time and whether these changes can be associated significantly with changing abiotic conditions. I then examine whether changes in invertebrate populations, which have previously been attributed to mouse predation, but with little explicit demographic analysis (see Crafford and Scholtz 1987; Chown and Smith 1993; Chown et al. 2002), can be associated with changing mouse populations, which I also show, remain major predators of invertebrates, as has been demonstrated previously (Gleeson and van Rensburg, 1982; Smith et al., 2002).

Methods

All field work was carried out on Marion Island (46°54'S, 37°45'E, Fig. 1), a volcanic island located approximately 2100 km southeast of Cape Town, South Africa. The island is uninhabited aside from a small, but continuous human presence associated with the meteorological station on the north-east coast. Marion Island has an oceanic climate (mean annual temperature *c*. 6.5°C, total precipitation of c. 1900 mm), but is currently experiencing rapid climate change. Since the late 1970s, when the effects of global dimming ceased counterbalancing rising temperatures (Hansen et al., 2006), mean annual temperature has increased by more than 1° C (le Roux and McGeoch, 2008) and the number of frost days dramatically declined (Huyser et al., 2000). Over the same period precipitation has declined by more than 800 mm and the duration of dry spells has increased (le Roux and McGeoch, 2008), leading to a significant reduction in peat moisture content (Chown and Smith, 1993). The island is characterised by two biomes; polar desert above 650 m a.s.l., and sub-Antarctic tundra below (Chown and Froneman, 2008). Five habitat complexes comprise the sub-Antarctic tundra biome; mire (wet peaty areas), slope (lowland areas with well-drained slopes), biotic (areas manured by seals and seabirds), saltspray (highly saline coastal herbfield), and fellfield (vascular plant cover dominated by cushions of *Azorella selago*).

Mice were likely introduced to Marion Island through sealing activity sometime after 1818 (Watkins and Cooper, 1986). The first demographic studies of the species occurred in the late 1970s (Berry et al., 1978; Gleeson, 1981) and focused in the three main habitats in which mice were found to live; mire, slope, and biotic. The timing of the breeding season varied between habitats and appeared correlated with invertebrate biomass, on which mice predominantly foraged. Populations peaked in summer and were followed by significant mortality in May/June (late summer/early winter). Domestic cats (*Felis catus* Linnaeus), present on Marion Island from 1949 to 1991, did not prey on mice to an extent that constrained the mouse population (van Aarde, 1980; van Aarde et al., 1996).

Studies throughout the 1980s and 1990s documented an increase in mouse impacts on the Marion Island environment, possibly associated with climate change (Crafford and Scholtz, 1987; Rowe-Rowe et al., 1989; Crafford, 1990; Smith and Steenkamp, 1990; Chown and Smith, 1993; Smith et al., 2002; Avenant and Smith, 2004). However, while mice may have increased their summer densities, in addition to their elevational range, between 1979 and 1991 (Matthewson and van Aarde, 1994; van Aarde et al., 1996), the population size was thought to be relatively stable between 1991 and 2001 (Ferreira et al., 2006).

Mouse trapping

Live trapping was conducted in 1991-92, 1993-94, 1996-97, 1998-99, and 2008-11. Trapping grids were placed within 1 km of the coastline in the mire, slope, and biotic habitats following Gleeson (1981). Trapping was limited to the eastern side of the island from 1991 to 1999, but included a mire and biotic site on the western side of the island in 2008-11 for a better understanding of whole-island mouse density. Trapping grid size, style of trap, the number of replicates, and trapping interval varied between years (Table 1). Traps within the grid were spaced 10 m apart regardless of grid size and trapping occurred for five successive nights (to complete one trapping "session"). From 1991-99 each trap was set for 6 h from sunset onwards and mice were marked by toe-clipping. From 2008-2011 each trap was active for 2 h from sunset onwards on five successive nights and mice were marked with stainless steel numbered ear tags.

Mice were sexed by anogenital distance (a standard animal husbandry technique) and mass measured to the nearest 0.5 g (Pesola 50-g scale; Baar, Switzerland). Breeding

status in female mice was assessed by the presence of a perforated vagina. Mice were separated into two age classes; juveniles (≤ 16 g, no perforated vagina in females) and subadults/adults (≥ 17g or perforated vagina in females). In 2008-11 the loss of previously applied ear tags was noted.

Mouse density

Mouse density was estimated using maximum-likelihood spatially explicit capture-recapture models (SECR, Borchers and Efford, 2008). Previous estimates of mouse populations on Marion Island (Gleeson, 1981; Matthewson and van Aarde, 1994; Ferreira et al., 2006) used conventional mark–recapture analyses that provide estimates of abundance (*N*) which can then be used to estimate population density (D) using the relation $\widehat{D} = \widehat{N}/A$ where *N* is the population size and *A* is the area occupied by the population. This method is prone to overestimation if the population is not geographically constrained, or capture probability varies because animals with only part of their home range within the array are available for capture (White et al., 1982). This "edge effect" can be corrected for by estimating the effective trapping area ($\hat{A}$) but most methods for determining $\hat{A}$ are considered imprecise (Jett and Nichols, 1987; Efford et al., 2004). SECR is a contemporary estimation approach that combines capture-recapture and distance sampling methods to estimate three model parameters; the probability of capture (*g0*), the spatial extent over which capture probability declines (σ), and population density (*D*). Density is defined as the number of home ranges whose centres are a realization of a homogeneous random spatial point process with intensity *D*. Distance sampling estimates the probability of detection of an individual as a function of distance from its range centre (a sub model rather than a single parameter; Efford et al., 2004; Borchers and Efford, 2008; Royle and Dorazio, 2008). As in conventional analysis, the populations are assumed closed (exempt from migration, death, and recruitment) for the duration of the session. I assumed a random (Poisson) distribution of range centres with a negative exponential detection function parameterised by the probability of capture (*g0*) and range size (*σ*). Even though this detection function suggests a positive detection probability for infinite distances, in practice distances are considered up to the point where they decline close enough to zero to have no further effect on the results. This distance is added as a buffer around the trapping array, which was set here to 300 m, after verifying that results were insensitive to wider buffers. Removals in the

population (i.e. accidental deaths during trapping) were assigned known capture histories of 0 with probability equals 1 following death. Replicate trapping grids were pooled when available, but sessions were not pooled as both *g0* and *σ* were found to vary considerably by season. Model selection was conducted using AIC and multimodel inference (Burnham and Anderson 2004) as well as visual inspection of the estimated parameters and standard errors for evidence of overparameterization and parameter nonidentifiability (Gimenez et al., 2004). Analyses were limited to those models that had a ΔAIC of < 7, as ΔAIC values > 7 contain little empirical support as the best model (Burnham and Anderson, 2002). All models were run in the statistical software R 2.15.0 (R Development Core Team, 2010) and the package *secr* (Efford, 2011).

The original mouse trapping data from 1979-80 was unavailable for SECR modelling. Density estimates from Gleeson (1981) were used when referencing this time period. These estimates were based on a modified Petersen Index and are likely overestimates of true density (Borchers and Efford, 2008).

Mouse phenology

To test for shifts in mouse breeding phenology the presence or absence of juvenile mice in the trappable population was used. Previous studies of Marion Island mice used the occurrence of pregnant females observed through dissection (Matthewson and van Aarde 1994; Avenant and Smith 2004). However, poor environmental conditions do not inhibit mice from attempting reproduction. Rather, mice practice both foetal absorption and facultative infanticide when energetically constrained (Perrigo, 1987). Thus, the ability of mice to successfully wean offspring is a more appropriate measurement of breeding conditions and phenology.

Mouse survival

Monthly survival was analysed separately for each habitat and year and pooled sessions when replicates were available. Maximum likelihood estimates were calculated for mouse survival using a 2-age (juveniles and subadults/adults) Cormack-Jolly-Seber (CJS) open population model (Lebreton et al., 1992). Local survival was estimated for years 1991-1999 only because tag loss between sessions was deemed too high in 2008-11 to yield meaningful

estimates. Directional tests (Z-tests) were undertaken using the program U-CARE 2.2.5 (Choquet et al., 2005) to test for transience and trap-dependence (Pradel, 1993; Pradel et al., 1997; Choquet et al., 2005). Model goodness-of-fit for the general model {ϕtpt}, where ϕ represents local survivor rate, p represents the encounter rate, and t represents time, was estimated by using the median ĉ procedure implemented in program MARK 6.2 (White and Burnham, 1999).

The presence of transients and trap-dependence was detected in all years, potentially underestimating the apparent survival of newly-marked individuals. To avoid this negative bias a "time since marking" (TSM) model (Pradel et al., 1997) was applied to subadults/adults. Trap dependence was accounted for by allowing the recapture probability to be a function of whether or not the individual was caught at the previous occasion, using previous capture status as individual covariates.

The possible relationships between survival and time (month), temperature (average daily minimum temperature between trapping periods), precipitation (total precipitation between trapping periods), invertebrate biomass, and mouse density were examined by adding them as covariates to the general survival model. "Trapping grid" was included for years that included replicate trapping grids. The Pearson correlation coefficient (r) was first used to examine the associations between the covariates. The selection criterion for the entry of the predictors into the models was set to a value of $p = 0.25$. Next, multicollinearity was controlled by requiring a variance inflation factor (VIF) to be less than five for each covariate. Model selection was based on Akaike's Information Criterion adjusted for overdispersion and sample size (QAICc, Burnham and Anderson, 2002). Variation in trapping dates did not allow for a month-by-month comparison of survival between years. Instead, survival models were constrained to give seasonal (winter: May-October, summer: November-April) estimates of mean monthly survival. All models were run in program MARK 6.2 (White and Burnham, 1999).

Effects of mouse phenology

Variation in mouse phenology was observed in the study. To explore the timing of the breeding season's impact on the Marion Island mouse population I used a 3-age (weaned juvenile, subadult, and adult) periodic matrix projection model (Caswell, 2001), with the

slope habitat in 1998-99 as an example. I assumed a pre-breeding census and one-month time step. The model is:

$$n_{t+1} = An_t \qquad \text{(equation 1)}$$

where *n* is a vector with the number of individuals in each age-class in month *t*, and *A* is the projection matrix

$$A = \begin{bmatrix} 0 & 0 & R \\ S_j & 0 & 0 \\ 0 & S_s & S_a \end{bmatrix} \qquad \text{(equation 2)}$$

In *A* I used the estimated survival rates for adult (S_a), subadult (S_s) and juvenile (S_j) mice from the best supported survival model (Supplementary Table A4), noting that subadults and adults were pooled and thus had the same survival estimates. *R* is calculated as the product of litter size * the probability of breeding. I used demographic data from 1991-92 (Matthewson and van Aarde, 1994) and assumed an average litter size of 7.24. I assumed an initial probability of breeding of 0.84, the estimated probability of mature (≥ 4-month old) mice. I decreased the probability of breeding to 0.52, the estimated probability across all age classes, after 8 weeks when young females began reaching sexual maturity. The outcomes of initiating breeding so that juveniles appear in February, January, and December, respectively, were examined. Input values and R code for the matrix model are presented in the Supplementary Material at Appendix A.

Diet analysis

To document current mouse diet, mice were snap-trapped every eight weeks in 2008-11. At least 15 baited snap-traps were deployed *ad hoc* at sunset and retrieved after 1-3 hours to minimize cannibalization of trapped mice. Trapping occurred in all three aforementioned habitat types on both the eastern and western sides of the island. Snap-trapped areas were at least 1 km distant from live-trapped grids.

Stomach content analysis followed the general methodology of Smith et al. (2002). Within 12 hours of emptying the snap-traps, mice were weighed (Pesola 50-g scale) and their stomachs removed and weighed (Mettler AE163 balance, ±0.1 mg). Stomach contents were sorted in a Petri dish under x10 or x25 magnification. The percentage contribution of each item to the volume of the particular stomach content (PV) was estimated to the nearest 5%. Percentage occurrence (PC) of a particular food item in a sampling period was

calculated from the number of stomachs it was found in and the number of stomachs examined. Diet variety was taken to be the number of diet items recorded in the sampling period and diet diversity was calculated, following Ebersole and Wilson (1980), as $1/\sum P_i^2$ where P_i (=PV/100) is the mean proportion of each of the diet items. An importance value (IV=PV*PC/100) was also calculated for each diet item (Cooper and Skinner, 1978). Relative importance value (RIV) of a particular item was taken as the importance value of that item expressed as a percentage of the sum of the importance values for all items ($100 \cdot IV/\sum IV$). Changes in mean RIV over time were assessed using two sample t-tests. Because RIVs are percentage data, values were logit-transformed prior to analysis (Warton and Hui, 2011).

Invertebrate biomass

Invertebrates were sampled in 1976-77 (Burger, 1978), 1996-97 (Hanel, 1999), and 2006-07 as part of a long-term assessment. Sampling occurred in the seven vegetation types that comprise the majority of the three habitats in which mice occur; *Sanionia uncinatus*, *Blepharidophyllum densifolium*, and *Jamesoniella colorata* (mire), *Blechnum penna-marina and Acaena magellanica* (slope), and *Cotula plumosa*, and *Poa cookii* (biotic). In 1976-77, 10 m x 10 m quadrates were selected at random in each habitat type at monthly intervals. From each of these, one circular (8 cm diameter) soil core was extracted randomly by using a circular corer. In 1996-97 and 2006-07, five 2 m x 2 m quadrates were staked out at random, and from each of these, two circular (7 cm diameter) soil cores were extracted randomly at bimonthly intervals using an O'Connor split corer. All core samples were hand-sorted in the laboratory. The sample was first sorted dry, and was subsequently washed to remove any remaining invertebrates. In 1996-97 and 2006-07 this hand-sorted and washed material was then placed in a Tullgren funnel for four days, after which remaining invertebrates were collected (mainly small chironomid larvae and spiders). All extracted invertebrates were identified to species or morphospecies where the former was not possible. The species were separated into their various developmental stages (adults or larvae) and then counted, weighed wet, and dried to constant mass at 60°C after which they were then weighed dry. In 1996-97 and 2006-07 soil worms were not dried so as to facilitate their later identification. Their dry mass was, however, estimated from a linear regression of dry mass on wet mass obtained from a separate sample of 20 earthworms that were subjected to the same treatment as the remaining invertebrates.

Analyses were limited to the macro-invertebrates that formed the major components of the mouse diet, pooled into five groups to match the taxonomic resolution of the original survey (Burger, 1978). The prey groups were lepidopteran larvae (*Pringleophaga marioni* and *Embryonopsis halticella*, of which the latter are generally rare in core samples owing to their monophagy of *Poa cookii*), weevil larvae (Curculionidae), weevil adults, soil worms (potworms and earthworms; Enchytraeidae and *Microscolex kerguelarum*), and spiders (*Myro spp.*, *Prinerigone vagans*). To facilitate comparison across datasets, 1976-77 data were converted to bimonthly estimates by taking the mean of the two months.

Differences in invertebrate biomass between sampling years were examined using a Kruskal-Wallis one-way analysis by ranks after Shapiro-Wilk Normality Tests rejected the assumption of normal distribution. Next, a multivariate approach was used to test for impacts of environmental variables on bimonthly estimates of invertebrate biomass. The patchy nature of Marion Island invertebrates resulted in "zero inflated" biomass data, meaning the number of zeros was too large to allow the response variable to be fit by using standard distributions (i.e., normal, Poisson, binomial, negative binomial, beta and gamma; Heilbron, 1994; Tu, 2002). Two approaches have been proposed to model zero inflated data: the mixture model approach and the two-part modelling approach (Cunningham and Lindenmayer, 2005; Martin et al., 2005). The mixture model approach assumes the response variable has a mixture distribution: with probability p it is equal to zero and with probability $1-p$ it has a Poisson or negative binomial distribution (Lambert, 1992). In the two-part conditional modelling approach the occurrence of zero observations and the positive abundances are separately modelled. The first part is a binary outcome logistic-type model and the second part is a truncated count model (Welsh et al., 1996) calibrated on available data. The two-part conditional modelling approach was used because it has two major advantages. First, the two aspects of the data can be modelled separately, and insight gained into whether they are being influenced by the covariates in different ways. Second, the analysis is simpler than the mixture model approach as the parameters for the two models can be estimated and interpreted independently (Welsh et al., 1996).

For each invertebrate group in each vegetation type, two data sets were created: one indicating whether the invertebrate group was present or not at each site, the other

showing the log-transformed biomass for those sites where the invertebrate group was present. These two data sets are hereafter referred to as the “presence data” and ”biomass given presence data”, respectively. Both the presence data and the biomass given presence data were modelled in terms of the predictor variables, using logistic and ordinary regression, respectively. Predictor variables were average seasonal mouse density, average temperature for the previous 30 days, total precipitation for the previous 30 days, and season (winter: May-October, summer: November-April) after being assessed for collinearity with the VIF and Pearson correlation matrix. There was little overlap between years that measured invertebrate biomass and mouse density. I therefore used mean seasonal mouse density estimates from 1979-80, 1998-99, and 2008-11 to represent densities in 1976-77, 1996-97, and 2006-07 respectively, assuming seasonal averages were representative of those years. All combinations of predictor variables were modelled and ranked by AIC_c. A relative importance value (RIV) for each variable was calculated by summing the Akaike weight (w_i) of every model in which it was included. Analyses were limited to those models that had a ΔAIC of < 7. The resulting values ranged from 0 to 1, with values closer to 1 indicating greater importance.

The logistic and ordinary regression models examining the relationship between invertebrate biomass and mouse density (biomass ~ mouse density) were then combined to model the expected invertebrate biomass in relation to mouse density following the method set out by Fletcher et al. (2005). Equations and R code for the two-part conditional model are presented in the Supplementary Material at Appendix B.

Results

Mouse density

Density estimates demonstrated an increase in the amplitude of population fluctuations between 1979-80 and 2008-11 (Supplementary Tables A1-A3). The late-summer/early winter die-offs that characterized the Marion Island mouse population continued in 2008-11, with winter densities higher or lower than those from the 1990s equally likely. However, peak summer density in the mire habitat increased twofold between 1993-94 and 1998-99 (Fig. 2a). The highest estimated density in 2008-11 (236.6 mice·ha^{-1}, 95% CI 158.8-352.5) was 84.1 % higher than the highest density in 1998-99 (128.5 mice·ha^{-1}, 95% CI 93.3-176.9). Peak

density in the slope habitat remained constant from 1991-92 to 1998-99, but increased fourfold between 1998-99 and 2008-11, peaking at 210.0 mice·ha^{-1} (95% CI 160.9-274.0) in 2010. Peak density in the eastern biotic trapping grid was highest in 1991-92 (246.6 mice·ha^{-1}, 95% CI 194.0-313.4), declined significantly in the mid and late 1990s, and increased again between 1998-99 (117.4 mice·ha^{-1}, 95% CI 74.3-185.7) and 2008-11 (222.4 mice·ha^{-1}, 95% CI 181.5-272.5). All model selection and estimates of *g0* and σ are presented in the Supplementary Material at Appendix C.

Mouse breeding phenology

A shift towards earlier breeding occurred in the Marion Island mouse population between 1979-80 and 2008-2011 (Fig 2b). Breeding phenology remained constant between 1979-80 and 1993-94 in the mire and slope habitats. The breeding season advanced in the mire habitat by two months between 1993-94 and 1998-99 and by an additional month between 1998-99 and 2008-11. The breeding season in the slope habitat advanced by one month between 1993-94 and 1998-99 and again between 1998-99 and 2008-2010. The breeding season in the biotic habitat showed more variation. Juveniles first appeared in December in 1979-80, 1993-94, and 1996-97. In 1991-92, 1998-99 and 2008-11 juveniles were first observed in November. Mice appeared to stop breeding in all habitats in late March or early April throughout the study period, estimated from when juveniles stopped appearing in traps and accounting for 6 weeks required for gestation and weaning (Berry, 1970).

Mouse survival

Model selection favoured a survival model that distinguished between age classes (Supplementary Table A4). Trapping grid, when applicable, was also highly supported. There was little trend among environmental covariates in predicting mouse survival, with high variation between top models between habitats and years. Mean monthly survival did not differ significantly between years for juvenile mice in any habitat as evidenced by overlap in confidence intervals (Fig. 3). Adult survival was significantly higher in the mire habitat during the summer season in 1998-99, and the biotic habitat during the winter in 1996-97. Adult winter survival in the slope habitat was significantly lower in 1991-92.

Effects of mouse phenology

The outcomes of the matrix model estimating the effects of phenology on mouse population density are presented in Fig. 6 and Supplementary Table A5. The matrix model estimated that in the absence of change to any other demographic parameter, the advancement of the breeding season from February (here, referring to the month in which juvenile mice first appear in traps) to January increased the number of juvenile and subadult/adult mice at peak density by 78.6 % and 81.0 %, respectively, for a total increase of 79.7 %. Initiating the breeding season in December resulted in the peak number of juvenile and subadult/adult mice increasing by 116.9 % and 203.2 %, respectively, for a total increase of 159.4 % from the original February start date.

Mouse diet

Mouse diet consisted primarily of invertebrates of which lepidopteran larvae had the highest mean annual RIV (Table 2). Between 1991-92 and 2008-11, the importance of lepidopteran larvae increased significantly in the mire habitat, while plant material significantly declined. The slope habitat had significant increases in the importance of lepidopteran larvae and spiders, with significant declines in weevil adults, larvae, and plant material. The importance of lepidopteran and weevil larvae increased in the biotic habitat, while weevil adults declined. Mouse diet variety decreased significantly in all habitats. There was a significant decrease in diet diversity in the slope and biotic habitats, but a significant increase in the mire habitat between study periods.

Invertebrate biomass

The majority of invertebrate groups experienced significant declines in all seven measured vegetation types (Fig. 4a-e). Kruskal-Wallis tests showed that biomass was significantly ($p < 0.05$) different between years for lepidopteran larvae in *S. uncinatus*, *A. magellanica*, *P. cookii*, *C. plumosa*, weevil adults in *C. plumosa*, weevil larvae in all vegetation types, soil worms in *S. uncinatus*, *J. colorata*, *B. penna-marina*, *A. magellanica*, *P. cookii*, *C. plumosa*, and spiders in *S. uncinatus*, *B. densifolium*, *J. colorata*, *A. magellanica*, and *P. cookii* (See Supplementary Table A6 for details). The lack of a significant difference in weevil adult biomass in most vegetation types is likely due to the considerable variation in the data considering their decline to the point of non-detection in *S. uncinatus*, *B. penna-marina*, and

P. cookii by 2006-07. The only species group to have a significant increase in biomass after 1996-97 was lepidopteran larvae in *C. plumosa* (t = -3.62, df = 9.83, $p < 0.01$).

Summing the Akaike weight (w_i) for each variable across all possible models for each species and habitat I found that mouse density was the most important explanatory variable in terms of both invertebrate presence and biomass (Table 3), acknowledging the lack of mouse density estimates specific to invertebrate sampling years. Mouse density and temperature each had the highest relative importance values (RIV) in 30.3 % of presence models, followed by season (24.2 %), and precipitation (15.2 %). Invertebrate biomass, given presence, was also best explained by mouse density, with the highest RIV in 33.3 % of models, followed by season (30.0 %), precipitation (20.0 %), and temperature (16.7 %).

The conditional models predicted a generally negative relationship between mice and invertebrates (Fig. 5). Biomass of all invertebrate species was predicted to decline in response to increased mouse density in the mire and slope habitats, with the exception of spiders in *B. densifolium* and weevil adults in *J. colorata*. Trends in the biotic habitat were less straightforward. Invertebrate biomass was predicted to decline in *C. plumosa*, with the exception of weevil adults and larvae. By contrast, invertebrate biomass was positively associated with mouse density in *P. cookii*.

Discussion

Despite decades of speculation that mice are increasing in density in the sub-Antarctic (Smith and Steenkamp, 1990), this study provides the first demonstration that this is the case, at least on Marion Island. Peak densities in the slope and mire habitats currently reach levels several times greater than those experienced in 1979-80 or the 1990s. This increase is coupled with a shift towards earlier breeding. An increase in peak density always followed an advanced breeding season, except for in two years. There was no significant increase in the biotic habitat in 1998-99 despite juveniles appearing in November. This may be explained by a change in the structure of the habitat (discussed further below). Peak density in the slope habitat in 1998-99 also failed to increase. However, it should be noted that juveniles were captured earlier on only one of the three trapping grids. When modelled separately, peak density was highest on the grid with juveniles appearing the earliest, though the difference was not significant.

An extended breeding season can have an especially profound effect on mouse density because it increases the possibility of adding additional sexually mature cohorts to the population before the cessation of the breeding season (Berry, 1968; Singleton et al., 2001; Mutze, 2009). This was demonstrated here by the matrix model (Fig. 6). Because female mice on Marion Island reach sexual maturity at four months old (but as young as two months; Matthewson and van Aarde 1994), initiating the breeding season earlier greatly increases the breeding population in the later breeding months. In turn, the total peak population is also greatly increased before the winter die-off. The importance of an extended breeding season in increasing density has been well-documented in other invasive house mouse populations (Pech et al., 1999; Singleton et al., 2001). However, such phenological changes have been almost exclusively linked to significant increases in food availability and quality (King, 1983; Bomford, 1987; Murphy, 1992), though the mechanisms that create such conditions may vary (Singleton et al., 2010). A search of the literature suggests that the extension of the breeding season on Marion Island is the first documented under decreased food availability.

The local effects of global climate change have warmed Marion Island considerably in the past few decades, with the warmest years on record occurring in the late 1990s (le Roux, 2008; Treasure and Chown, 2012). The reproductive seasonality of house mice in cold climates, including Southern Ocean islands, is governed by the interaction between temperature and energy intake (Bronson 1979; Manning and Bronson 1990) rather than photoperiod (Pryor and Bronson, 1981). Because of their relatively high surface-to-volume ratio, mice are highly susceptible to heat loss and must commit a significant proportion of energy into maintaining homeostasis. For example, starved laboratory mice kept at 11° C will exhaust their fat reserves within 1.5 days and a single missed feeding period under such temperatures may result in death (Bronson, 1987). This demand competes with the cost of reproduction which is exceptional in rodents. For example, lactation requires at least double the energy intake of a non-breeding female (Speakman, 2008) and can be four or five times higher under cooler conditions (Bronson, 1985). For mice to extend their breeding season, a significant increase in energy intake, or decrease in the cost of thermoregulation must occur. The decline in invertebrate biomass on Marion Island limits the likelihood of an

earlier breeding season being the product of increased foraging proficiency, leaving ameliorating environmental conditions as the likeliest mechanism.

Of at least equal importance to lessening the energetic costs of mice on Marion Island is the persistent drying of the island (le Roux and McGeoch, 2008). Wetting reduces thermal resistance by half and leads to increased energy costs (Webb and King, 1984; McArthur and Ousey, 1994; McCafferty et al., 1997), especially in juveniles (Webb et al., 1990). In this regard, drier conditions are likely to have a significant impact on breeding, survival, and juvenile recruitment. This is especially significant in the mire habitat where the decline in precipitation has led to a significant loss in peat moisture content (Chown and Smith, 1993) and may explain why the greatest changes in breeding advancement, and density occurred in this habitat. The benefit of a consistently drier island may explain why changes in mouse density and phenology have progressed steadily despite variation in temperature between years.

This study was unable to determine the importance of survival in regulating the Marion island mouse population. While its role in determining winter densities is straightforward, how survival in the summer season contributes to density is less clear. Although it has been suggested that survival is the main driver of population increases in small mammals, including mice (Korpimäki et al., 2004), rodent-specific studies have found it only of minor importance when compared to changes in reproduction (Singleton et al., 2010). For house mice specifically, Mutze (2009) found adult survival to have no significant influence on plague outbreaks in Australian cropland, but that juvenile survival was a vital parameter, presumably because of the aforementioned recruitment of juveniles into the breeding population within the season. Unfortunately the high confidence limits on juvenile survival in the 1990s and the lack of estimates from 2008-11 makes it impossible to speculate on its importance on Marion Island. Nevertheless, it should at least be considered that in addition to an extended breeding season, increased juvenile survival may also play a role in the observed increases in density.

A number of further changes in Marion Island mouse population dynamics owing to climate change are plausible. For example, litter size is likely to have increased as lessened energy constraints curtail the occurrence of foetal absorption and facultative infanticide

(Perrigo, 1987; van Aarde and Jackson, 2007). Likewise, age of sexual maturity may also have advanced to reflect that of populations in more favourable environments (Berry, 1970; Efford, 1988). Drier conditions could also greatly improve the quality and quantity of available mouse burrows in previously marginal habitat (Avenant and Smith, 2003; Ferreira et al., 2006). However, the present study could not distinguish these possible additional changes.

Despite enabling higher peak densities, ameliorating environmental conditions failed to lessen the extent of the May/June die-offs long observed in the Marion Island mouse population. Marion Island mice are not cold adapted (Webb et al., 1997) and the number of very cold wind-chill events has not changed over the past five decades (le Roux and McGeoch, 2008). Additionally, the monthly rate of warming on the island is variable, with June exhibiting the lowest temperature increase of all months (le Roux, 2008), and seasonal invertebrate biomass also reaches its nadir at this time (Smith et al., 2002). Thus, mice still experience the same number of extreme cold events as in earlier decades, while both the seasonal and long-term decline in invertebrate biomass makes offsetting the increased cost of metabolism more difficult. As long as this continues to occur on Marion Island, die-offs can be expected. However, on mouse-invaded Southern Ocean islands with milder climates, such as Gough Island, mice do not exhibit as severe a seasonal decline (Cuthbert and Hilton, 2004) suggesting continued warming, drying, or changes in wind patterns could further alter mouse population dynamics.

The biotic habitat showed the least change in phenology and was the lone habitat in which peak mouse density was highest in a year other than 2008-11. This is possibly due to a vegetation shift. Tussock grassland is the preferred habitat of invasive mice on Southern Ocean islands (Berry et al., 1979; Pye, 1993; Harper, 2010; Russell, 2012), where well-drained and sheltered conditions allow burrows to reach several degrees warmer than external ambient temperatures (Pye et al. 1999). On Marion Island the substantial loss of manuring seabirds due to cat predation has caused a significant decline in tussock grassland which has largely been replaced by *P. annua* lawn (Gremmen and Smith, 2008). *Poa annua* offers little to mice in terms of cover and may explain why peak densities in this habitat declined when others increased. It also appears that densities are again on the rise, and that ameliorating conditions may have begun to compensate for any negative effects of this

change in habitat structure. Regardless, current densities lower than in previous years in the biotic habitat are unlikely to offer any form of indemnity to the Marion Island ecosystem. The habitat represents just 3.5 % of the island surface area below 300 m a.s.l. while slope and mire represent 18.7% and 17.7%, respectively (Gremmen and Smith, 2008). Adjusting for area, the total number of mice below 300 m on Marion Island at peak density more than doubled between 1998-99 and 2008-11 (Table 4).

There was a considerable shift in the importance of prey items in mouse diets between 1991-92 and 2008-11. Lepidopteran larvae continued to be the dominant prey item and increased in importance despite strong declines in biomass. This may be due to even greater losses in other prey items, specifically weevil adults which appear to have declined to an extent where they no longer represent a significant portion of mouse diet. The decline in the importance of plant material was unexpected in view of invertebrate declines. Given the option, Marion Island mice will select invertebrate prey over plant material (Smith et al., 2002). Higher temperatures and the decline in rainfall and snow cover may allow mice to forage outside of burrows more frequently and efficiently, lessening mouse reliance on seed caches (van Aarde and Jackson, 2007). Mouse-driven declines in preferred plant species such as the sedge *Uncinia compacta* (Smith and Steenkamp, 1990; Chown and Smith, 1993) may also play a role.

The two-part conditional models emphasized the importance of mouse density in influencing invertebrate biomass and demonstrated a predominantly negative relationship between predator and prey. The exception was for *P. cookii* vegetation, within which mouse density had a positive association for all invertebrate groups. In addition to the aforementioned shelter and burrowing advantages, the shoot-base of *P. cookii* is rich in stored soluble carbohydrates and along with preformed flowers can provide an important food source (Berry et al., 1979). Indeed, tussock grass is the staple diet of rodents on other Southern Ocean islands (Pye et al., 1999) and plant matter continues to be an important food resource for Marion Island mice in the biotic habitat. It is possible that mice do not occur in *P. cookii* vegetation to forage for invertebrates alone and that the same structure and cover that encourages high invertebrate biomass also contributes to high mouse density. At least for the former, it is clear that *P. cookii* grasslands support high densities and

species numbers of both macro- and micro-invertebrates (Burger, 1978; Gabriel et al., 2001; Barendse et al., 2002).

The arrival of invasive mice on Marion Island predates the baseline data for invertebrate biomass by over 150 years. Disregarding the likely detrimental impacts that occurred during this undocumented period, the changes in invertebrate biomass since the 1970s (Table 5) are exceptional. If the surface area occupied by each of the three studied habitats below 300 m is considered, the estimated total island invertebrate biomass loss is 86.1% and 89.8% in the winter and summer respectively.

Invertebrate biomass on Marion Island appears insufficient to sustain high mouse densities for more than a few months of the year, contributing to an annual late-summer population crash. While mouse densities are considerably lower until the following breeding season, even low densities can suppress the recovery of invertebrate populations (St Clair, 2011). The steady and precipitous decline in invertebrate biomass suggests that the invertebrate population on the island cannot sufficiently recover from the preceding year's predation. Extended mouse breeding seasons and potentially higher peak densities are likely to compound the problem, raising the question of what further declines in invertebrate biomass will bring. A possible window to Marion Island's future can be found on Gough Island, South Atlantic Ocean. A large portion of the Gough Island invasive mouse population survives the winter, possibly due to milder environmental conditions (Cuthbert and Hilton, 2004). Low availability of invertebrates and seeds in the winter months causes food limitation and leads to mouse attacks on the island's avifauna (Angel and Cooper, 2006). As a result, mouse-induced mortality is contributing to population declines in Tristan albatross (*Diomedea dabbenena* Mathews), Gough bunting (*Rowettia goughensis* Clarke), Atlantic petrel (*Pterodroma incerta* Schlegel), and potentially other burrowing seabirds (Cuthbert and Hilton, 2004; Wanless et al., 2009, 2012). A similar outcome is within reason for Marion Island and both the increased occurrence of vertebrate tissue in mouse stomachs observed in this study and the recent increase in the number of mouse attacks on seabirds (Wanless et al., 2007; Jones and Ryan, 2009) support the hypothesis.

This study is in keeping with a growing body of research demonstrating the significant direct impacts of mice on the Marion Island ecosystem. For instance, the size-

selective foraging behaviour of mice has changed the body size of its preferred prey species and potentially interfered with the evolution of the island's invertebrate fauna by halting speciation in the weevil *Ectemnorhinus similis* species complex (Chown, 1990; Chown and Smith, 1993; Treasure and Chown, 2012). Moreover, mouse herbivory has greatly reduced the sedge *U. compacta* (Smith and Steenkamp, 1990; Chown and Smith, 1993) and burrowing causes widespread damage to *A. selago*, a keystone plant species (Phiri et al., 2008). However, the most profound impact of mice may be indirect. There is increasing evidence that invasive predators on islands are capable of initiating landscape-level trophic cascades, where through the predation of an intermediate organism, they indirectly affect the abundance and composition of the vegetative community (Croll et al., 2005; Kurle et al., 2008; Wardle et al., 2009). The majority of studies have focussed on seabird predation and the interruption of marine to terrestrial nutrient transfer (Fukami et al., 2006; Maron et al., 2006; Towns et al., 2009), but Marion Island mice may present another form of the phenomenon. As the primary drivers of nutrient cycling and energy flow on the island, reductions in invertebrate biomass undoubtedly exacerbate nutrient limitation in an already impoverished system. A reduction in nutrient cycling can be expected to decrease litter nutrient quality and primary productivity and enhance the rate of peat accumulation (Smith and Steenkamp, 1990). Peat accumulation in turn drives vegetation succession and ecosystem structure through control of the hydrological regime (Gremmen, 1981). Potential mitigating effects of warming such as increased soil fauna activity and decomposition rates (Smith and Steenkamp, 1990; Aerts, 2006; Bokhorst et al., 2007) are complex and likely to be insufficient given the scale of invertebrate loss. Thus, invasive mice may be the instigators of a trophic cascade shaping basic ecosystem processes on Marion Island.

Conclusion

The present results highlight the growing concern regarding the interaction between climate change and invasive species on the Southern Ocean islands and have far-reaching implications for the region. All Southern Ocean islands have their unique characteristics (size, age, geology, established alien species, etc.), but also share a fundamental ecology of high primary production, slow decomposition, and reliance upon invertebrates for nutrient cycling (Smith and Steenkamp, 1990). Mice have been introduced to at least 11 Southern

Ocean islands (Angel et al., 2008) and notable impacts have been reported on plant (Smith and Steenkamp, 1990; Jones et al., 2003; Phiri et al., 2008), invertebrate (Copson, 1986; Chown and Smith, 1993; Marris, 2000; Le Roux et al., 2002; St Clair, 2011; Russell, 2012), and avian communities (Huyser et al., 2000; Cuthbert and Hilton, 2004; Miskelly et al., 2006; Wanless et al., 2007). The current situation on Marion Island suggests that as climate change continues to create ameliorating conditions for mice the severity of these impacts will increase. Further, these impacts are greatest when mice are the sole invasive mammal present on an island, a situation becoming more common as eradication efforts remove other alien predators but spare mice (Angel et al., 2008). From the perspective of conservation, it is vital that mice be given equal consideration as other invasive mammals when considering eradication for island restoration.

References

van Aarde, R.J., 1980. The diet and feeding behaviour of feral cats, *Felis catus* at Marion Island. South African Journal of Wildlife Research 10, 123–128.

van Aarde, R.J., Ferreira, S.M., Wassenaar, T.D., Erasmus, D.G., 1996. With the cats away the mice may play. South African Journal of Science 92, 357–358.

van Aarde, R.J., Jackson, T.P., 2007. Food, reproduction and survival in mice on sub-Antarctic Marion Island. Polar Biology 30, 503–511.

Aerts, R., 2006. The freezer defrosting: global warming and litter decomposition rates in cold biomes. Journal of Ecology 94, 713–724.

Anderson, A., 2002. Faunal collapse, landscape change and settlement history in remote oceania. World Archeaology 33, 375–390.

Angel, A., Cooper, J., 2006. A review of the impacts of introduced rodents on the islands of Tristan and Gough. Royal Society for the Protection of Birds, Report No. 17.

Angel, A., Wanless, R.M., Cooper, J., 2008. Review of impacts of the introduced house mouse on islands in the Southern Ocean: are mice equivalent to rats? Biological Invasions 11, 1743–1754.

Athens, J.S., 2009. *Rattus exulans* and the catastrophic disappearance of Hawai'i's native lowland forest. Biological Invasions 11, 1489–1501.

Atkinson, I.A.E., 1985. The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifaunas, in: Moors, P.J. (Ed.), Conservation of Island Birds.

Cambridge: International Council for Bird Preservation Technical Publication No. 3, pp. 35–81.

Avenant, N.L., Smith, V.R., 2003. The microenvironment of house mice on Marion Island (sub-Antarctic). Polar Biology 26, 129–141.

Avenant, N.L., Smith, V.R., 2004. Seasonal changes in age class structure and reproductive status of house mice on Marion Island (sub-Antarctic). Polar Biology 27, 99–111.

Bailey, E.P., 1993. Introduction of foxes to Alaskan Islands — History, effects on avifauna, and eradication. United States Department of the Interior Fish and Wildlife Service Resource Publication 193.

Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., Good, J.E.G., Harrington, R., Hartley, S., Jones, T.H., Lindroth, R.L., Press, M.C., Symrnioudis, I., Watt, A.D., Whittaker, J.B., 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biology 8, 1–16.

Barendse, J., Mercer, R.D., Marshall, D.J., 2002. Habitat specificity of mites on sub-Antarctic Marion Island. Environmental Entomology 31, 612–625.

Benning, T.L., LaPointe, D., Atkinson, C.T., Vitousek, P.M., 2002. Interactions of climate change with biological invasions and land use in the Hawaiian Islands: modeling the fate of endemic birds using a geographic information system. Proceedings of the National Academy of Sciences of the U.S.A. 99, 14246–14249.

Bergstrom, D.M., Chown, S.L., 1999. Life at the front: history, ecology and change on Southern Ocean islands. Trends in Ecology and Evolution 14, 472–477.

Bergstrom, D.M., Lucieer, A., Kiefer, K., Wasley, J., Belbin, L., Pedersen, T.K., Chown, S.L., 2009. Indirect effects of invasive species removal devastate World Heritage Island. Journal of Applied Ecology 46, 73–81.

Berry, R.J., 1968. The ecology of an island population of the house mouse. Journal of Animal Ecology 37, 445–470.

Berry, R.J., 1970. The natural history of the house mouse. Field Study 3, 219–262.

Berry, R.J., Bonner, W.N., Peters, J., 1979. Natural selection in house mice (*Mus musculus*) from South Georgia (South Atlantic Ocean). Journal of Zoology 189, 385–398.

Berry, R.J., Peters, J., van Aarde, R.J., 1978. Sub-antarctic house mice: colonization, survival and selection. Journal of Zoology 184, 127–141.

Bester, M.N., Bloomer, J.P., Bartlett, P.A., Muller, D.D., van Rooeyn, M., Buchner, H., 2000. Final eradication of feral cats from sub-Antarctic Marion Island, southern Indian Ocean. South African Journal of Wildlife Research 30, 53–57.

Blackburn, T.M., Cassey, P., Duncan, R.P., Evans, K.L., Gaston, K.J., 2004. Avian extinction and mammalian introductions on oceanic islands. Science 305, 1955–1958.

Bokhorst, S., Huiskes, A., Convey, P., Aerts, R., 2007. Climate change effects on organic matter decomposition rates in ecosystems from the Maritime Antarctic and Falkland Islands. Global Change Biology 13, 2642–2653.

Bomford, M., 1987. Food and reproduction of wild house mice. 1. Diet and breeding seasons in various habitats on irrigated cereal farms in New South Wales. Australian Wildlife Research 14, 183–196.

Borchers, D.L., Efford, M.G., 2008. Spatially explicit maximum likelihood methods for capture-recapture studies. Biometrics 64, 377–385.

Bronson, F.H., 1979. The reproductive ecology of the house mouse. Quarterly Review of Biology 54, 265–299.

Bronson, F.H., 1985. Mammalian reproduction: An ecological perspective. Biology of Reproduction 32, 1–26.

Bronson, F.H., 1987. Susceptibility of the fat reserves of mice to natural challenges. Journal of Comparative Physiology B 157, 551–554.

Bronson, F.H., 2009. Climate change and seasonal reproduction in mammals. Philosophical Transactions of the Royal Society B 364, 3331–3340.

Broome, K.G., 2009. Managing invasive animals on sub-Antarctic islands. Papers and Proceedings of the Royal Society of Tasmania 143, 53–55.

Burger, A.E., 1978. Terrestrial invertebrates: a food resource for birds at Marion Island. South African Journal of Antarctic Research 8, 87–99.

Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: a practical information-theoretic approach., 2nd ed. Springer, New York.

Burnham, K.P., Anderson, D.R., 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociological Methods and Research 33, 261–304.

Carlquist, S., 1974. Island biology. Columbia University Press, New York.

Caswell, H., 2001. Matrix population models, 2nd ed. Sinauer, Sunderland.

Choquet, R., Reboulet, A., Lebreton, J.D., Gimenez, O., Pradel, R., 2005. U-CARE 2.2 User's Manual. CEFE, UMR 5175, CNRS, Montpellier, France.

Chown, S.L., 1990. Speciation in the sub-Antarctic weevil genus *Dusmoecetes* Jeannel (Coleoptera: Curculionidae). Systematic Entomology 15, 283–296.

Chown, S.L., Convey, P., 2007. Spatial and temporal variability across life's hierarchies in the terrestrial Antarctic. Philosophical Transactions of the Royal Society B 362, 2307–2331.

Chown, S.L., Froneman, P.W., 2008. The Prince Edward Islands: land-sea interactions in a changing ecosystem. Sun Press, Stellenbosch.

Chown, S.L., McGeoch, M.A., Marshall, D.J., 2002. Diversity and conservation of invertebrates on the sub-Antarctic Prince Edward Islands. African Entomology 10, 67–82.

Chown, S.L., Rodrigues, A.S.L., Gremmen, N.J.M., Gaston, K.J., 2001. World heritage status and conservation of Southern Ocean islands. Conservation Biology 15, 550–557.

Chown, S.L., Smith, V.R., 1993. Climate change and the short-term impact of feral house mice at the sub-Antarctic Prince Edward Islands. Oecologia 96, 508–516.

Convey, P., 2010. Terrestrial biodiversity in Antarctica – Recent advances and future challenges. Polar Science 4, 135–147.

Convey, P., 2011. Antarctic terrestrial biodiversity in a changing world. Polar Biology 34, 1629–1641.

Cooper, R.L., Skinner, J.D., 1978. Importance of termites in the diet of the aardwolf *Proteles cristatus* in South Africa. South African Journal Of Zoology 14, 5–8.

Copson, G., 1986. The diet of the introduced rodents *Mus musculus* L and *Rattus rattus* L on Sub-Antarctic Macquarie Island. Australian Wildlife Research 13, 441 – 445.

Courchamp, F., Chapuis, J., Pascal, M., 2003. Mammal invaders on islands: impact, control and control impact. Biological Reviews 78, 347–383.

Cox, P.M., Betts, R.A., Jones, C.D., Spall, S.A., Totterdell, I.J., 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature 408, 184–187.

Crafford, J.E., 1990. The role of feral house mice in ecosystem functioning on Marion Island, in: Kerry, K., Hempel, G. (Eds.), Antarctic Ecosystems: Ecological Change and Conservation. Springer-Verlag, Berlin, pp. 359–364.

Crafford, J.E., Scholtz, C.H., 1987. Quantitative differences between the insect faunas of Sub-Antarctic Marion and Prince Edward Islands: a result of human intervention? Biological Conservation 40, 255–262.

Croll, D.A., Maron, J.L., Estes, J.A., Danner, E.M., Byrd, G. V, 2005. Introduced predators transform subarctic islands from grassland to tundra. Science 307, 1959–1961.

Cunningham, R.B., Lindenmayer, D.B., 2005. Modeling count data of rare species: some statistical issues. Ecology 86, 1135–1142.

Cuthbert, R., Hilton, G., 2004. Introduced house mice *Mus musculus*: a significant predator of threatened and endemic birds on Gough island, South Atlantic Ocean. Biological Conservation 117, 483–489.

Darwin, C., 1859. On the origin of species, 1st ed. John Murray, London.

Delong, K.T., 1967. Population ecology of feral house mice. Ecology 48, 611–634.

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C., Martin, P.R., 2008. Impacts of climate warming on terrestrial ectotherms across latitude. Proceedings of the National Academy of Sciences of the U.S.A. 105, 6668–6672.

Diamond, J., 2007. Easter Island revisited. Science 317, 1692–1694.

Dukes, J.S., Mooney, H.A., 1999. Does global change increase the success of biological invaders? Trends in Ecology and Evolution 14, 135–139.

Ebbert, S.E., Byrd, G. V, 2000. Eradications of invasive species to restore natural biological diversity on Alaska Maritime National Wildlife Refuge, in: Veitch, D., Clout, M.N. (Eds.), Turning the Tide: The Eradication of Invasive Species. UK: IUCN SSC Invasive Species Specialist Group, IUCN, Gland, Switzerland and Cambridge, UK, pp. 102–109.

Ebersole, J.P., Wilson, J.C., 1980. Optimal foraging: the responses of *Peromyscus leucopus* to experimental changes in processing time and hunger. Ecology 46, 80–85.

Efford, M.G., 1988. Population ecology of *Mus musculus* on Mana Island, New Zealand. Journal of Zoology 216, 539–563.

Efford, M.G., 2011. secr: spatially explicit capture–recapture models. R package version, 2(2).

Efford, M.G., Dawson, D.K., Robbins, C.S., 2004. DENSITY: software for analysing capture – recapture data from passive detector arrays. Animal Biodiversity and Conservation 1, 217–228.

Ferreira, S.M., van Aarde, R.J., Wassenaar, T.D., 2006. Demographic responses of house mice to density and temperature on sub-Antarctic Marion Island. Polar Biology 30, 83–94.

Fletcher, D., MacKenzie, D., Villouta, E., 2005. Modelling skewed data with many zeros: A simple approach combining ordinary and logistic regression. Environmental and Ecological Statistics 12, 45–54.

Frenot, Y., Chown, S.L., Whinam, J., Selkirk, P.M., Convey, P., Skotnicki, M., Bergstrom, D.M., 2005. Biological invasions in the Antarctic: extent, impacts and implications. Biological Reviews 80, 45–72.

Fukami, T., Wardle, D.A., Bellingham, P.J., Mulder, C.P.H., Towns, D.R., Yeates, G.W., Bonner, K.I., Durrett, M.S., Grant-Hoffman, M.N., Williamson, W.M., 2006. Above- and below-ground impacts of introduced predators in seabird-dominated island ecosystems. Ecology Letters 9, 1299–1307.

Gabriel, A.G.A., Chown, S.L., Barendse, J., Marshall, D.J., Mercer, R.D., Pugh, P.J.A., Smith, V.R., 2001. Biological invasions of Southern Ocean islands: the Collemhola of Marion Island as a test of generalities. Ecography 24, 421–430.

Gimenez, O., Viallefont, A., Catchpole, E.A., Choquet, R., Morgan, B.J.T., 2004. Methods for investigating parameter redundancy. Animal Biodiversity and Conservation 27, 1–12.

Gleeson, J.P., 1981. Ecology of the house mouse *Mus musculus* Linnaeus, on Marion Island. MSc. thesis, University of Pretoria, South Africa.

Gleeson, J.P., van Rensburg, P.J.J., 1982. Feeding ecology of the house mouse *Mus musculus*, on Marion Island. South African Journal of Antarctic Research 12, 34–39.

Gremmen, N.J.M., 1981. The vegetation of the Subantarctic islands Marion and Prince Edward. Geobotany 3, 1–149.

Gremmen, N.J.M., Smith, V.R., 2008. Terrestrial vegetation and dynamics, in: Chown, S.L., Froneman, P.W. (Eds.), The Prince Edward Islands: Land-sea Interactions in a Changing Ecosystem. Sun Press, Stellenbosch, pp. 215–244.

Hanel, C., 1999. The distribution and abundance of macro-invertebrates in the major vegetation communities of Marion Island and the impact of alien species. MSc. thesis, University of Pretoria, South Africa.

Hansen, J., Sato, M., Ruedy, R., Lo, K., Lea, D.W., Medina-Elizade, M., 2006. Global temperature change. Proceedings of the National Academy of Sciences of the U.S.A. 103, 14288–14293.

Harper, G.A., 2010. Habitat use by mice during winter on Subantarctic Auckland Island. New Zealand Journal of Ecology 34, 262–264.

Heilbron, D.C., 1994. Zero-altered and other regression models for count data with added zeros. Biometrical Journal 36, 531–547.

Honêk, A., 1996. Geographic variation in thermal requirements for insect development. European Journal of Entomology 93, 303–312.

Howard, W.E., 1951. Relation between low temperature and available food to survival of small rodents. Journal of Mammalogy 32, 300–312.

Huyser, O., Ryan, P.G., Cooper, J., 2000. Changes in population size, habitat use and breeding biology of lesser sheathbills (*Chionis minor*) at Marion Island: impacts of cats, mice and climate change? Biological Conservation 92, 299–310.

Ingram, J.C., Dawson, T.P., 2005. Climate change impacts and vegetation response on the island of Madagascar. Proceedings of the Royal Society A 363, 55–59.

Jett, D.A., Nichols, J.D., 1987. A field comparison of nested grid and trapping web density estimators. Journal of Mammalogy 68, 888–892.

Jones, A.G., Chown, S.L., Gaston, K.J., 2003. Introduced house mice as a conservation concern on Gough Island. Biodiversity and Conservation 12, 2107–2119.

Jones, H.P., Tershy, B.R., Zavaleta, E.S., Croll, D.A., Keitt, B.S., Finkelstein, M.E., Howald, G.R., 2008. Severity of the effects of invasive rats on seabirds: a global review. Conservation Biology 22, 16–26.

Jones, M.G.W., Ryan, P.G., 2009. Evidence of mouse attacks on albatross chicks on sub-Antarctic Marion Island. Antarctic Science 22, 39–42.

Kennedy, A.D., 1995. Antarctic terrestrial ecosystem response to global environmental change. Annual Review of Ecology and Systematics 26, 683–704.

King, C.M., 1983. The relationship between beech (*Nothofagus sp.*) seedfall and populations of mice (*Mus musculus*), and the demographic and dietary responses of stoasts (*Mustula erminea*), in three New Zealand forests. Journal of Animal Ecology 52, 141–166.

King, W.B., 1985. Island birds: will the future repeat the past?, in: Conservation of Island Birds. ICBP Technical Publication No. 3, pp. 3–15.

Korpimäki, E., Brown, P.R., Jacob, J., Pech, R.P., 2004. The puzzles of population cycles and outbreaks of small mammals solved? Bioscience 54, 1071–1079.

Kurle, C.M., Croll, D.A., Tershy, B.R., 2008. Introduced rats indirectly change marine rocky intertidal communities from algae- to invertebrate-dominated. Proceedings of the National Academy of Sciences of the U.S.A. 105, 3800–3804.

Lambert, D., 1992. Zero-inflated Poisson regression, with an application to defects in manufacturing. Technometrics 34, 1–14.

Lebreton, J., Burnham, K.P., Clobert, J., Anderson, D.R., 1992. Modeling survival and testing biological hypotheses using marked animals - a unified approach with case studies. Ecological Monographs 62, 67–118.

Loehle, C., Eschenbach, W., 2012. Historical bird and terrestrial mammal extinction rates and causes. Diversity and Distributions 18, 84–91.

Losos, J.B., Jackman, T.R., Larson, A., de Queiroz, K., Rodriguez-Schettino, L., 1998. Contingency and determinism in replicated adaptive radiations of island lizards. Science 279, 2115–2118.

MacArthur, R.H.W., Wilson, E.O., 1967. The theory of island biogeography. Princeton University Press, Princeton.

Major, H.L., Jones, I.L., Byrd, G.V., Williams, J.C., 2006. Assessing the effects of introduced Norway rats (*Rattus norvegicus*) on survival and productivity of least auklets. Auk 123, 681–694.

Manning, J.M., Bronson, F.H., 1990. The effects of low temperature and food intake on ovulation in domestic mice. Physiological Zoology 63, 938–948.

Maron, J.L., Estes, J.A., Croll, D.A., Danner, E.M., Elmendorf, S.C., Buckelew, S.L., 2006. An introduced predator alters Aleutian Island plant communities by thwarting nutrient subsidies. Ecological Monographs 76, 3–24.

Marris, J.W.M., 2000. The beetle (Coleoptera) fauna of the Antipodes Islands, with comments on the impact of mice; and an annotated checklist of the insect and arachnid fauna. Journal of the Royal Society of New Zealand 30, 169–195.

Martin, T.G., Wintle, B.A., Rhodes, J.R., Kuhnert, P.M., Field, S.A., Low-Choy, S.J., Tyre, A.J., Possingham, H.P., 2005. Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. Ecology Letters 8, 1235–1246.

Matthewson, D.C., van Aarde, R.J., 1994. Population biology of house mice (*Mus musculus* L.) on sub-Antartic Marion Island. South African Journal Of Zoology 29, 1–9.

McArthur, A.J., Ousey, J.C., 1994. Heat loss from a wet animal: changes with time in the heat balance of a physical model representing a newborn homeotherm. Journal of Thermal Biology 19, 81–89.

McCafferty, D.J., Moncrieff, J.B., Taylor, I.R., 1997. The effect of wind speed and wetting on thermal resistance of the barn owl (*Tyto alba*) II: coat resistance. Journal of Thermal Biology 22, 265–273.

McGeoch, M.A., Butchart, S.H.M., Spear, D., Marais, E., Kleynhans, E.J., Symes, A., Chanson, J., Hoffmann, M., 2010. Global indicators of biological invasion: species numbers, biodiversity impact and policy responses. Diversity and Distributions 16, 95–108.

Medina, F.M., Bonnaud, E., Vidal, E., Tershy, B.R., Zavaleta, E.S., Josh Donlan, C., Keitt, B.S., Corre, M., Horwath, S. V., Nogales, M.M., 2011. A global review of the impacts of invasive cats on island endangered vertebrates. Global Change Biology 17, 3503–3510.

Milberg, P., Tyrberg, T., 1993. Naive birds and noble savages - a review of man-caused prehistoric extinctions of island birds. Ecography 16, 229–250.

Miskelly, C.M., Walker, K.J., Elliott, G.P., 2006. Breeding ecology of three Subantarctic snipes (genus *Coenocorypha*). Notornis 53, 361–374.

Mulder, C.P.H., Grant-Hoffman, M.N., Towns, D.R., Bellingham, P.J., Wardle, D.A., Durrett, M.S., Fukami, T., Bonner, K.I., 2008. Direct and indirect effects of rats: does rat eradication restore ecosystem functioning of New Zealand seabird islands? Biological Invasions 11, 1671–1688.

Murphy, E.C., 1992. The effects of a natural increase in food supply on a wild population of house mice. New Zealand Journal Of Ecology 16, 33–40.

Mutze, G.J., 2009. Changes in body condition and body size affect breeding and recruitment in fluctuating house mouse populations in south-eastern Australia. Austral Ecology 34, 278–293.

Nogales, M., Mart, A., Tershy, B.R., Donlan, C.J., Veitch, D., 2004. A review of feral cat eradication on islands. Conservation Biology 18, 310–319.

Paulay, G., 1994. Biodiversity on oceanic islands: its origin and extinction. American Zoologist 34, 134–144.

Pech, R.P., Hood, G.M., Singleton, G.R., Salmon, E., Forrester, R.I., Brown, P.R., 1999. Models for predicting plagues of house mice (*Mus domesticus*) in Australia, in: Singleton, G.R., Hinds, L., Leirs, H., Zhang, Z. (Eds.), Ecologically-based Rodent Management. ACIAR, Canberra, Australi, pp. 81–112.

Perrigo, G., 1987. Breeding and feeding strategies in deer mice and house mice when females are challenged to work for their food. Animal Behaviour 35, 1298–1316.

Phiri, E.E., McGeoch, M.A., Chown, S.L., 2008. Spatial variation in structural damage to a keystone plant species in the sub-Antarctic: interactions between *Azorella selago* and invasive house mice. Antarctic Science 21, 189–196.

Pradel, R., 1993. Flexibility in survival analysis from recapture data: handling trap dependence, in: Lebreton, J.D., North, P.M. (Eds.), Marked Individuals in the Study of Bird Populations. Birkh Verlag, Basel, pp. 29–37.

Pradel, R., Hines, J.E., Lebreton, J., Nichols, J.D., 1997. Capture-recapture survival models taking account of transients. Biometrics 53, 60–72.

Pryor, S., Bronson, F.H., 1981. Relative and combined effects of low temperature, poor diet, and short daylength on the productivity of wild house mice. Biology of Reproduction 25, 734–743.

Pye, T., 1993. Reproductive biology of the feral house mouse (*Mus musculus*) on Subantarctic Macquarie Island. Wildlife Research 20, 745–758.

Pye, T., Swain, R., Seppelt, R.D., 1999. Distribution and habitat use of the feral black rat (*Rattus rattus*) on subantarctic Macquarie Island. Journal of Zoology 247, 429–438.

R Development Core Team, 2010. R: A language and environment for statistical computing. http://www.r-project.org.

Ricklefs, R.E., Lovette, I.J., 1999. The roles of island area *per se* and habitat diversity in the species-area relationships of four Lesser Antillean faunal groups. Journal of Animal Ecology 68, 1142–1160.

Rignot, E., Kanagaratnam, P., 2006. Changes in the velocity structure of the Greenland Ice Sheet. Science 311, 986–990.

le Roux, P.C., 2008. Climate and climate change, in: Chown, S.L., Froneman, P.W. (Eds.), The Prince Edward Islands: Land-Sea Interactions in a Changing Ecosystem. Sun Press, Stellenbosch, pp. 39–64.

le Roux, P.C., McGeoch, M.A., 2008. Changes in climate extremes, variability and signature on sub-Antarctic Marion Island. Climatic Change 86, 309–329.

le Roux, V., Chapuis, J., Frenot, Y., Vernon, P., 2002. Diet of the house mouse (*Mus musculus*) on Guillou Island, Kerguelen archipelago, Subantarctic. Polar Biology 25, 49–57.

Rowe-Rowe, D.T., Green, B., Crafford, J.E., 1989. Estimated impact of feral house mice on Sub-Antarctic invertebrates at Marion Island. Polar Biology 9, 457–460.

Royle, J.A., Dorazio, R.M., 2008. Hierarchical models of animal abundance and occurrence. Journal of Agricultural, Biological, and Environmental Statistics 11, 249–263.

Russell, J.C., 2012. Spatio-temporal patterns of introduced mice and invertebrates on Antipodes Island. Polar Biology 35, 1187–1195.

Singleton, G., Krebs, C.J., Davis, S., Chambers, L., Brown, P., 2001. Reproductive changes in fluctuating house mouse populations in southeastern Australia. Proceedings of the Royal Society B 268, 1741–1748.

Singleton, G.R., Belmain, S.R., Brown, P.R., Hardy, B., 2010. Rodent outbreaks: ecology and impacts. International Rice Research Institute, Los Banos, Phillipines.

Singleton, G.R., Brown, P.R., Pech, R.P., Jacob, J., Mutze, G.J., Krebs, C.J., 2005. One hundred years of eruptions of house mice in Australia – a natural biological curio. Biological Journal of the Linnean Society 84, 617–627.

Smith, V.R., 2002. Climate change in the sub-Antarctic: an illustration from Marion Island. Climatic Change 52, 345–357.

Smith, V.R., Avenant, N.L., Chown, S.L., 2002. The diet and impact of house mice on a sub-Antarctic island. Polar Biology 25, 703–715.

Smith, V.R., Mucina, L., 2006. Vegetation of subantarctic Marion and Prince Edward Islands, in: Mucina, L., Rutherford, M.C. (Eds.), The Vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, pp. 698–723.

Smith, V.R., Steenkamp, M., 1990. Climatic change and its ecological implications at a Subantarctic island. Oecologia 85, 14–24.

Speakman, J.R., 2008. The physiological costs of reproduction in small mammals. Philosophical Transactions of the Royal Society B 363, 375–398.

St Clair, J.J.H., 2011. The impacts of invasive rodents on island invertebrates. Biological Conservation 144, 68–81.

Steadman, D.W., 1995. Prehistoric extinctions of Pacific island birds: biodiversity meets zooarchaeology. Science 267, 1123–1131.

Towns, D.R., Wardle, D.A., Mulder, C.P.H., Yeates, G.W., Fitzgerald, B.M., Parrish, G.R., Bellingham, P.J., Bonner, K.I., 2009. Predation of seabirds by invasive rats: multiple indirect consequences for invertebrate communities. Oikos 118, 420–430.

Treasure, A.M., Chown, S.L., 2012. Antagonistic effects of temperature change and biological invasion on ectotherm body size. in press.

Tu, W., 2002. Zero-inflated data, in: El-Shaarawi, A.H., Peiegorsch, W.W. (Eds.), Encyclopedia of Envirometrics. John Wiley and Sons, Chichester.

Veitch, C.R., 2001. The eradication of feral cats (*Felis catus*) from Little Barrier Island, New Zealand. New Zealand Journal of Zoology 28, 1–12.

Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 1997. Human domination of Earth's ecosystems. Science 277, 494–499.

Wallace, A.R., 1881. Island life: or, the phenomena and causes of insular faunas and floras, including a revision and attempted solution of the problem of geological climates. Harper, London.

Walsh, J.C., Venter, O., Watson, J.E.M., Fuller, R.A., Blackburn, T.M., Possingham, H.P., 2012. Exotic species richness and native species endemism increase the impact of exotic species on islands. Global Ecology and Biogeography 21, 841–850.

Walther, G., Roques, A., Hulme, P.E., Sykes, M.T., Pysek, P., Kühn, I., Zobel, M., Bacher, S., Botta-Dukát, Z., Bugmann, H., Czúcz, B., Dauber, J., Hickler, T., Jarosík, V., Kenis, M., Klotz, S., Minchin, D., Moora, M., Nentwig, W., Ott, J., Panov, V.E., Reineking, B., Robinet, C., Semenchenko, V., Solarz, W., Thuiller, W., Vilà, M., Vohland, K., Settele, J., 2009. Alien species in a warmer world: risks and opportunities. Evolution 24, 686–693.

Wanless, R.M., Angel, A., Cuthbert, R.J., Hilton, G.M., Ryan, P.G., 2007. Can predation by invasive mice drive seabird extinctions? Biology Letters 3, 241–244.

Wanless, R.M., Ratcliffe, N., Angel, A., Bowie, B.C., Cita, K., Hilton, G.M., Kritzinger, P., Ryan, P.G., Slabber, M., 2012. Predation of Atlantic petrel chicks by house mice on Gough Island. Animal Conservation 15, 472–479.

Wanless, R.M., Ryan, P.G., Altwegg, R., Angel, A., Cooper, J., Cuthbert, R., Hilton, G.M., 2009. From both sides: dire demographic consequences of carnivorous mice and longlining for the Critically Endangered Tristan albatrosses on Gough Island. Biological Conservation 142, 1710–1718.

Wardle, D.A., Bellingham, P.J., Bonner, K.I., Mulder, C.P.H., 2009. Indirect effects of invasive predators on litter decomposition and nutrient resorption on seabird-dominated islands. Ecology 90, 452–464.

Wardle, D.A., Bellingham, P.J., Fukami, T., Mulder, C.P.H., 2007. Promotion of ecosystem carbon sequestration by invasive predators. Biology Letters 3, 479–82.

Warton, D.I., Hui, F.K.C., 2011. The arcsine is asinine: the analysis of proportions in ecology. Ecology 92, 3–10.

Watkins, B.P., Cooper, J., 1986. Introduction, present status and control of alien species at the Prince Edward Islands, sub-Antarctic. South African Journal of Antarctic Research 16, 86–94.

Webb, D.R., King, J.R., 1984. Effects of wetting of insulation of bird and mammal coats. Journal of Thermal Biology 9, 189–191.

Webb, D.R., Porter, W.P., McClure, P.A., 1990. Development of insulation in juvenile rodents: functional compromise in insulation. Functional Ecology 4, 251–256.

Webb, P.I., Ellison, G.T.H., Skinner, J.D., van Aarde, R.J., 1997. Are feral house mice from the sub-Antarctic adapted to cold? International Journal of Mammalian Biology 62, 58–62.

Welsh, A.H., Cunningham, R.B., Donnelly, C.F., Lindenmayer, D.B., 1996. Modelling the abundance of rare species: statistical models for counts with extra zeros. Ecological Modelling 88, 297–308.

White, G.C., Anderson, D.R., Burnham, K.P., Otis, D.L., 1982. Capture–recapture and removal methods for sampling closed populations. Los Alamos National Laboratory Rep. LA-8787-NERP. Los Alamos, NM, USA.

White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:S1, S120:S139.

Whittaker, R.J., Fernández-Palacios, J.M., 2007. Island biogeography. Ecology, evolution and conservation. Oxford University Press, Oxford, UK.

Zavaleta, E.S., Hobbs, R.J., Mooney, H.A., 2001. Viewing invasive species removal in a whole-ecosystem context. Trends in Ecology and Evolution 16, 454–459.

Tables

Table 1: Live trapping periods and methodology on Marion Island for 1991-92, 1993-94, 1996-97, 1998-99, and 2008-11. Trap type refers to single or multi-capture traps. Multi* refers to a grid that was trapped with single capture traps, cleared, and trapped at least one more time within the same night. In this instance traps were treated as multi-captures following (Efford, 2011). Location refers to the eastern or western side of the island.

Habitat	Trapping Period	Trapping Interval (weeks)	Trapping Grid Size (traps)	Trap Type	Grids Trapped (Replicates)	Location
Mire	Jun 1991 to Feb 1992	8	10 x 10	Single	1	East
	May 1993 to Apr 1994	4	10 x 10	Single	1	East
	Jun 1996 to Mar 1997	8	7 x 7	Multi*	2	East
	Apr 1998 to Apr 1999	4	7 x 7	Single	2	East
	Sep 2008 to Feb 2011	8	7 x 7	Multi	1	East
	Sep 2008 to Feb 2011	8	7 x 7	Multi	1	West
Slope	May 1991 to Mar 1992	4	10 x 10	Single	1	East
	May 1993 to Apr 1994	4	10 x 10	Single	1	East
	Apr 1998 to Apr 1999	4	7 x 7	Single	3	East
	Sep 2008 to Feb 2011	8	7 x 7	Multi	1	East
Biotic	May 1991 to Mar 1992	4	10 x 10	Single	1	East
	May 1993 to Apr 1994	4	10 x 10	Single	1	East
	May 1996 to May 1997	8	7 x 7	Multi*	2	East
	Apr 1998 to Apr 1999	4	7 x 7	Single	2	East
	Aug 2008 to Feb 2011	8	7 x 7	Multi	1	East
	Sep 2008 to Feb 2011	8	7 x 7	Multi	1	West

Table 2: Annual mean relative importance values (RIV) of diet items in the mire, slope, and biotic habitats on Marion Island in 1992-93 and 2008-11. RIVs consist of frequency and volume of occurrence in the diet and sum to 100 per column. Mean diet variety and diversity are also presented. The ± values represent standard deviations. Data from 1992-93 were extracted from Smith *et al.* (2002). The "other prey" group refers to other species of invertebrates including mites, aphids, and flies as well as mouse hair and feathers. The "unknown vertebrate" group refers to mammal and/or avian tissue (muscle, adipose, etc.).

	Food Item	1992-93		2008-11		*df*	*t*	*p*
Mire	Lepidopteran larvae	59.2	± 23.8	74.0	± 18.9	320	6.89	<0.001
	Weevil larvae	8.1	± 12.5	8.0	± 7.7	320	0.04	0.970
	Weevil adults	8.1	± 6.5	4.8	± 7.0	320	1.47	0.146
	Soil worms	2.1	± ??[a]	1.6	± 1.9	320		NA
	Spiders	0.7	± ??	6.9	± 1.6	320		NA
	Plants	15.7	± 2.1	1.7	± 1.8	320	4.10	<0.001
	Unknown vertebrate	0.0		1.5	± 2.1	320		NA
	Other Prey	5.9	± ??	1.6	± 3.5	320		NA
	Mean Diet Variety	8.2	± 0.7	2.3	± 0.3	320	100.77	<0.001
	Mean Diet Diversity	2.8	± 0.2	3.6	± 0.3	320	-19.23	<0.001
Slope	Lepidopteran larvae	11.8	± 15.2	50.4	± 31.5	290	-13.85	<0.001
	Weevil larvae	12.0	± 16.1	4.0	± 3.4	290	3.07	0.003
	Weevil adults	20.0	± 16.8	1.6	± 1.8	290	6.00	<0.001
	Soil worms	0.9	± ??	2.8	± 5.7	290		NA
	Spiders	2.6	± 4.0	6.1	± 8.4	290	-2.59	0.010
	Plants	48.4	± 33.9	22.0	± 33.5	290	13.56	<0.001
	Unknown vertebrate	0.0		4.3	± 5.3	290		NA
	Other Prey	4.5	± ??	8.9	± 21.8	290		NA
	Mean Diet Variety	8.2	± 0.7	2.4	± 0.6	290	70.73	<0.001
	Mean Diet Diversity	3.6	± 0.3	3.0	± 0.9	290	5.91	<0.001
Biotic	Lepidopteran larvae	45.1	± 21.3	52.4	± 28.2	424	-2.12	0.036
	Weevil larvae	3.9	± 7.6	16.7	± 19.4	424	-7.12	<0.001
	Weevil adults	6.9	± 8.1	0.3	± 0.4	424	4.46	<0.001
	Soil worms	9.2	± 19.9	5.6	± 10.8	424	1.91	0.060
	Spiders	0.4	± ??	0.1	± 0.1	424		NA
	Plants	22.6	± 20.2	20.7	± 18.8	424	0.56	0.578
	Unknown vertebrate	0.0		3.3	± 3.5	424		NA
	Other Prey	11.9	± ??	0.9	± 2.1	424		NA
	Mean Diet Variety	11.6	± 0.6	1.9	± 0.4	424	161.45	<0.001
	Mean Diet Diversity	4.4	± 0.3	3.1	± 0.8	424	12.55	<0.001

[a] The data was presented in Smith et al. (2002) in such a way that it was not possible to extract standard deviation

Table 3: Overall importance of mouse density, season, temperature, and precipitation in describing bimonthly invertebrate presence, and biomass given presence within the seven measured vegetation types on Marion Island. The importance value equals the sum of the Akaike weights (w_i) across candidate models containing the given variable. The w_i ranges from 0 to 1, with values closer to 1 being more important. The variable with the highest importance value is highlighted in grey. Missing values (NA) are where too few invertebrates were recorded to complete the model, with the exception of soil worms in *S. uncinatus* where the presence model failed due to linear separation, and soil worms in *B. densifolium* where the error distribution of the biomass given presence model remained non-parametric after log transformation.

Habitat	Vegetation	Invertebrate Group	Logistic regression (presence)				Ordinary regression (biomass)			
			Mouse density	Season	Temp-erature	Precip-itation	Mouse density	Season	Temp-erature	Precip-itation
Mire	*S. uncinatus*	Lepidopteran larvae	1.000	0.664	0.833	0.982	0.730	0.417	0.449	0.469
		Weevil adults	NA				NA			
		Weevil larvae	0.903	0.386	0.403	0.365	0.467	0.369	0.368	0.315
		Soil worms	NA				0.417	0.761	0.431	0.453
		Spiders	0.602	0.476	1.000	0.849	0.282	0.297	0.875	1.000
	B. densifolium	Lepidopteran larvae	0.404	0.848	0.353	0.296	0.522	0.663	0.301	0.260
		Weevil adults	0.977	0.350	0.495	0.340	0.322	0.310	0.776	0.142
		Weevil larvae	0.617	0.743	0.381	0.302	0.446	0.567	0.348	0.315
		Soil worms	0.380	0.412	0.418	0.344	NA			
		Spiders	0.350	0.875	1.000	0.913	0.250	0.467	0.372	0.990
	J. colorata	Lepidopteran larvae	0.356	0.550	0.610	0.321	0.313	0.208	0.212	0.267
		Weevil adults	0.345	0.461	0.323	0.964	0.209	0.306	0.444	0.208
		Weevil larvae	0.297	1.000	1.000	0.250	0.874	0.527	0.808	0.272
		Soil worms	0.922	0.470	0.425	0.695	0.499	0.590	0.345	0.574
		Spiders	0.312	0.677	0.677	0.361	0.758	0.527	0.406	0.991
Slope	*B. penna-marina*	Lepidopteran larvae	NA				NA			

		Weevil adults	NA				NA			
		Weevil larvae	NA				NA			
		Soil worms	0.832	0.430	0.323	0.277	0.405	0.305	0.379	0.547
		Spiders	0.392	0.371	0.365	0.363	0.550	0.167	0.511	0.173
	A. magellanica	Lepidopteran larvae	0.618	0.581	0.475	0.489	0.584	0.120	0.157	0.140
		Weevil adults	0.579	0.434	0.405	0.362	0.980	0.137	0.104	0.265
		Weevil larvae	0.973	0.536	0.375	0.260	0.251	0.296	0.427	0.920
		Soil worms	0.786	0.366	0.407	0.321	1.000	0.283	0.946	0.340
		Spiders	0.847	0.852	0.954	0.265	0.509	0.632	0.497	0.649
Biotic	*P. cookii*	Lepidopteran larvae	0.337	0.496	0.355	0.580	0.689	1.000	0.979	0.949
		Weevil adults	0.360	0.421	0.313	0.653	0.220	0.236	0.343	0.202
		Weevil larvae	0.492	0.332	0.624	0.743	0.789	0.985	0.689	0.224
		Soil worms	0.343	0.703	0.500	0.484	0.407	0.319	0.876	0.647
		Spiders	0.261	0.745	1.000	0.280	1.000	0.885	0.959	1.000
	C. plumosa	Lepidopteran larvae	0.340	0.311	0.319	0.671	0.332	0.638	0.521	0.318
		Weevil adults	0.392	1.000	1.000	0.829	0.851	0.110	0.204	0.563
		Weevil larvae	0.948	0.472	1.000	0.953	0.526	0.937	0.858	0.201
		Soil worms	0.346	0.435	0.361	0.391	0.348	0.612	0.409	0.315
		Spiders	0.412	0.515	0.373	0.324	0.329	0.979	1.000	0.789

Table 4: Estimated total number of mice present below 300 m a.s.l in the mire, slope, and biotic habitats on Marion Island at peak density from 1979-80 to 2008-11.

Year	Mire	Slope	Biotic	Total
1979-80	122 500	121 730	87 990	332 220
1993-94	227 040	177 775	93 882	511 819
1998-99	449 651	185 179	82 214	717 043
2008-11	828 150	776 902	155 687	1 760 740

Table 5: Estimated change in invertebrate biomass (kg·ha^{-1} ± SD) in the mire, slope, and biotic habitats on Marion Island between 1976-77 (baseline), 1996-97, and 2006-07.

	Winter			Summer		
Year	Mire	Slope	Biotic	Mire	Slope	Biotic
1976-77	51.8 ± 68.0	49.3 ± 26.6	376.4 ± 202.6	83.4 ± 107.0	58.1 ± 50.1	305.2 ± 106.9
1996-97	6.1 ± 5.9	37.9 ± 26.7	167.9 ± 83.8	9.9 ± 5.2	60.7 ± 59.4	226.4 ± 168.7
2006-07	1.7 ± 3.2	16.4 ± 21.7	60.3 ± 43.7	2.3 ± 2.1	7.1 ± 7.8	52.4 ± 23.4
Percentage loss from baseline	96.7%	66.8%	84.0%	97.3%	87.7%	82.8%

Figure Legends

Figure 1: Sub-Antarctic vegetation zones on Marion Island as provided by Smith and Mucina (2006). Coastal vegetation refers to biotic and saltspray communities. Arrows indicate the general area of the mouse trapping program on the east and west coasts of the island. Inset: Marion Island's position (red) in relation to Antarctica and other Southern Ocean Islands.

Figure 2: a, Estimated peak density of mice·ha^{-1} (± 95% CI) on Marion Island, 1979-2011. Estimates for 1996-97 and 1998-99 were each pooled across replicates. Estimates for 1979-80 were based on a modified Petersen Index and are likely an overestimate of true density, whereas the other estimates were based on spatially explicit capture recapture methods and likely unbiased. b, First appearance of juvenile mice in the trappable population in the mire (blue), slope (orange), and biotic (green) habitats on Marion Island, 1979-2011. Circles indicate years in which trapping occurred.

Figure 3: Mean monthly survival of juvenile and adult mice during the summer and winter seasons on Marion Island, 1991-92 to 1998-1999. Estimates are from 2-age class models corrected for transience and trap dependence with monthly survival parameters constrained to have constant winter and summer survival.

Figure 4: Mean annual biomass (mg/m^2 ± SD) of a) lepidopteran larvae, b) weevil larvae, c) weevil adults, d) soil worms, and e) spiders on Marion Island in 1976-77, 1996-97, and 2006-07 in *S. uncinatus* (San), *B. densifolium* (Blep), *J. colorata* (Jam), *B. penna-marina* (Blec), *A. magellanica* (Aca), *P. cookii* (Poa), and *C. plumosa* (Cot) vegetation. Stars indicate significant differences in invertebrate biomass between sampling periods. Values and analyses are presented in Supplementary Table A6.

Figure 5: Expected biomass of the five main invertebrate prey groups plotted against mouse density in the seven measured vegetation types on Marion Island. The shaded areas represent 95% confidence intervals. Plots in blue and marked with an asterisk represent the probability of presence only and are presented where too few invertebrate captures occurred to model biomass given presence. Blanks occur where too few captures occurred to model the probability of presence and/or biomass given presence with the exception of soil worms in *S. uncinatus* where the presence model failed due to linear separation.

Figure 6: Estimated impact of phenology in the Marion Island mouse population based on the matrix population model. Earlier breeding resulting in the first appearance of juvenile mice in December, January and February are represented by green, purple, and blue respectively. Solid and dashed lines indicate the number of subadults/adults and juveniles, respectively. Values are presented in Supplementary Table A5.

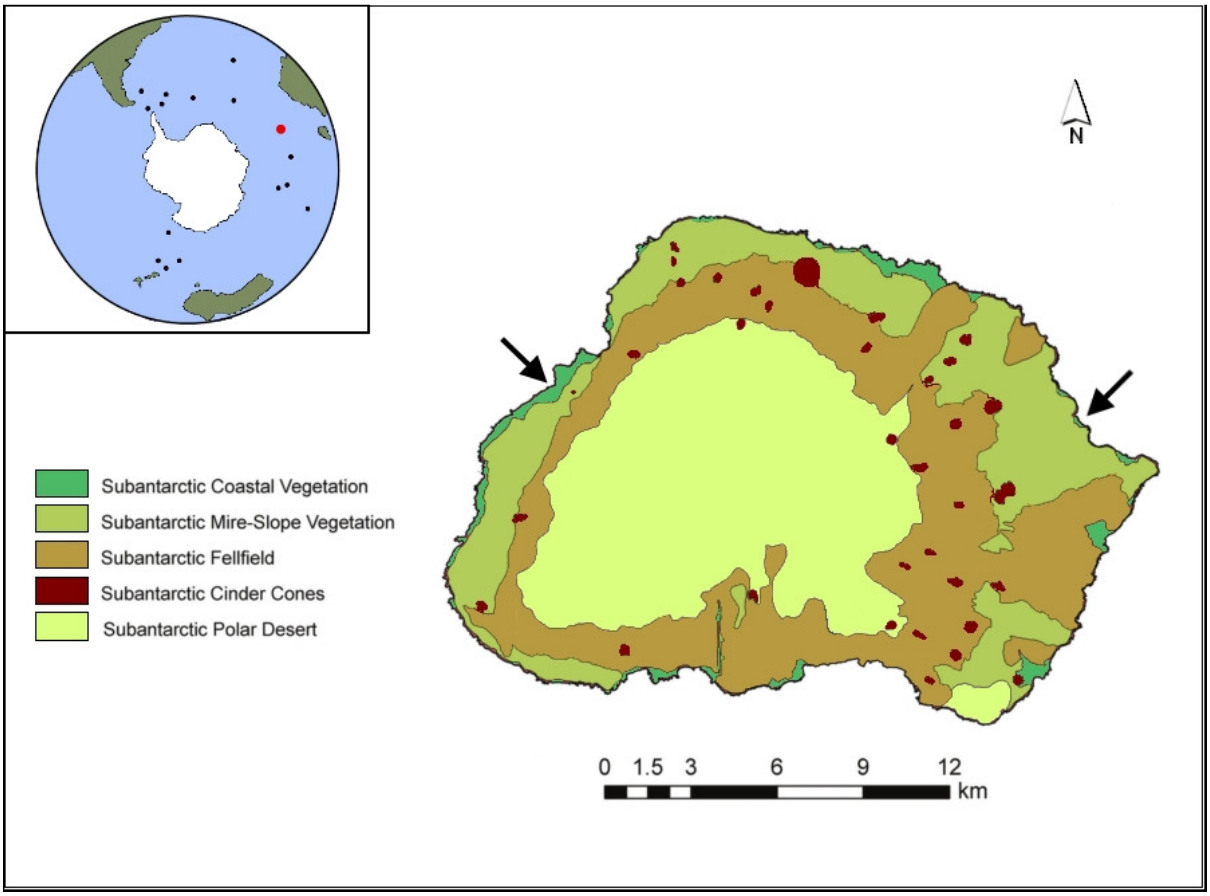


Figure 1

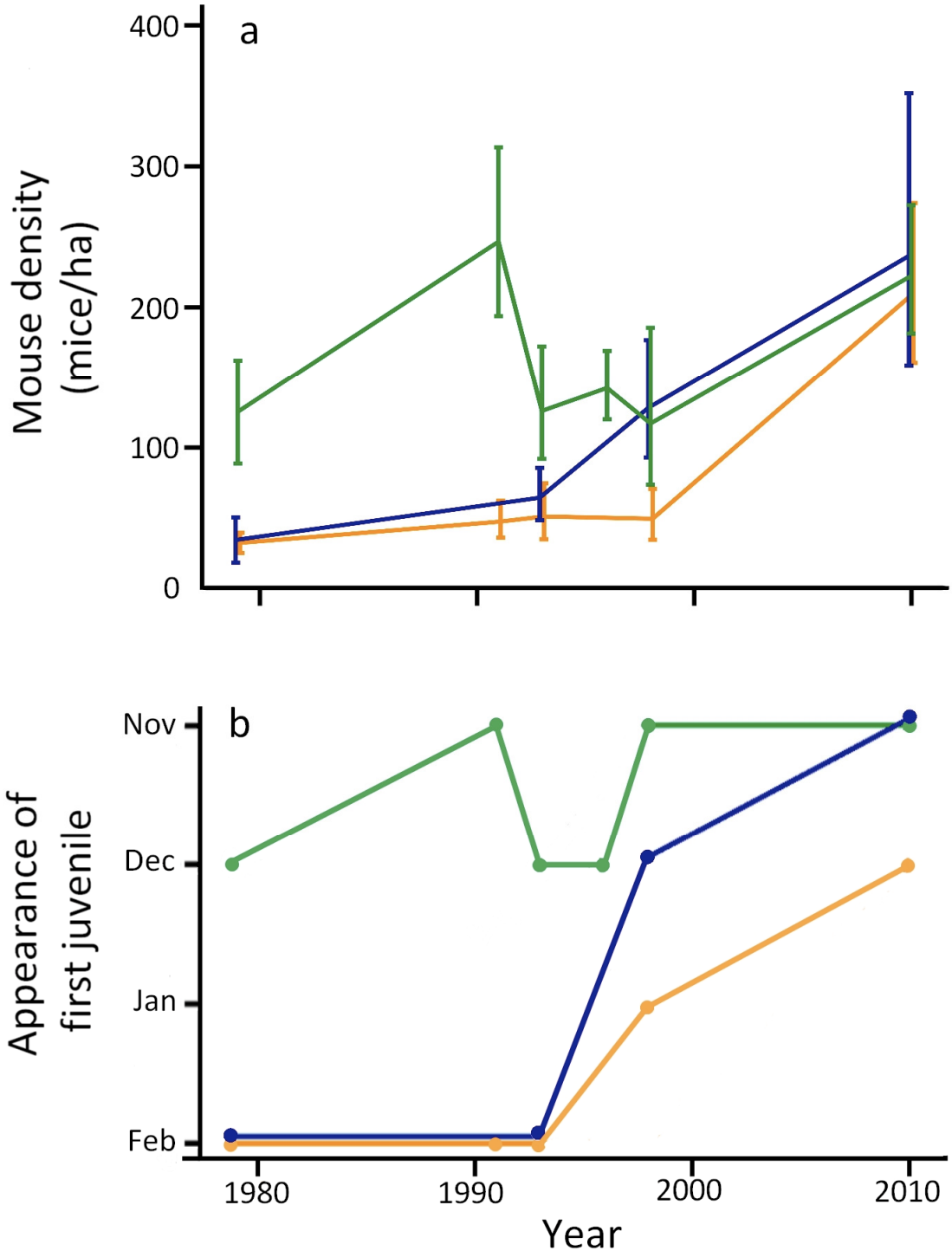


Figure 2

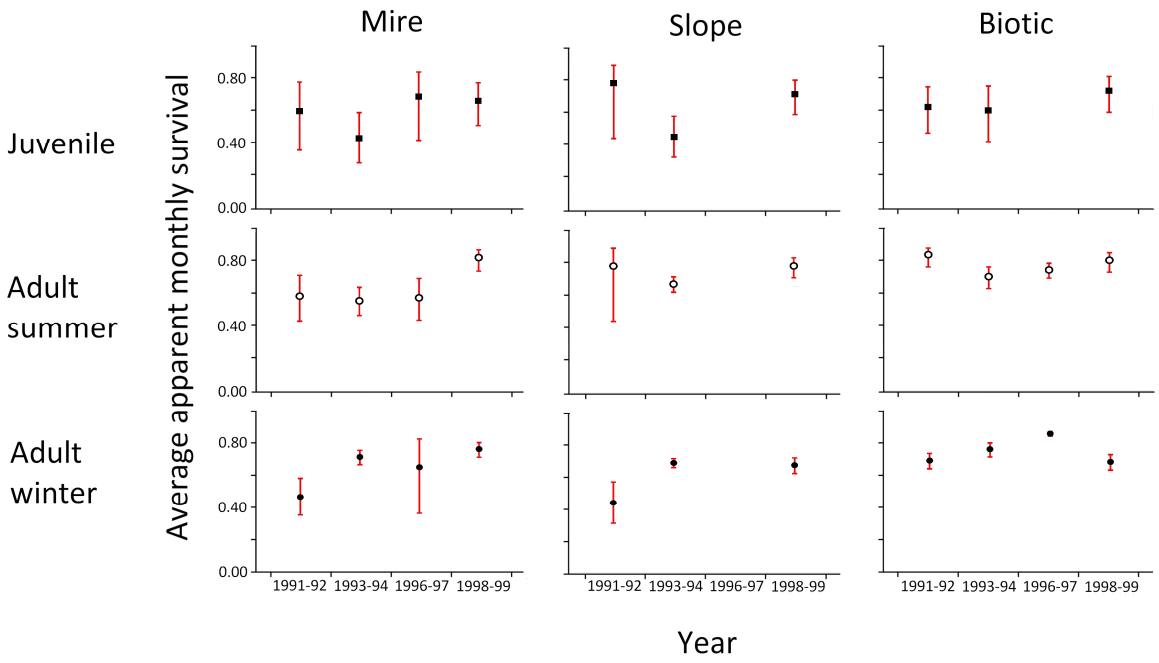


Figure 3

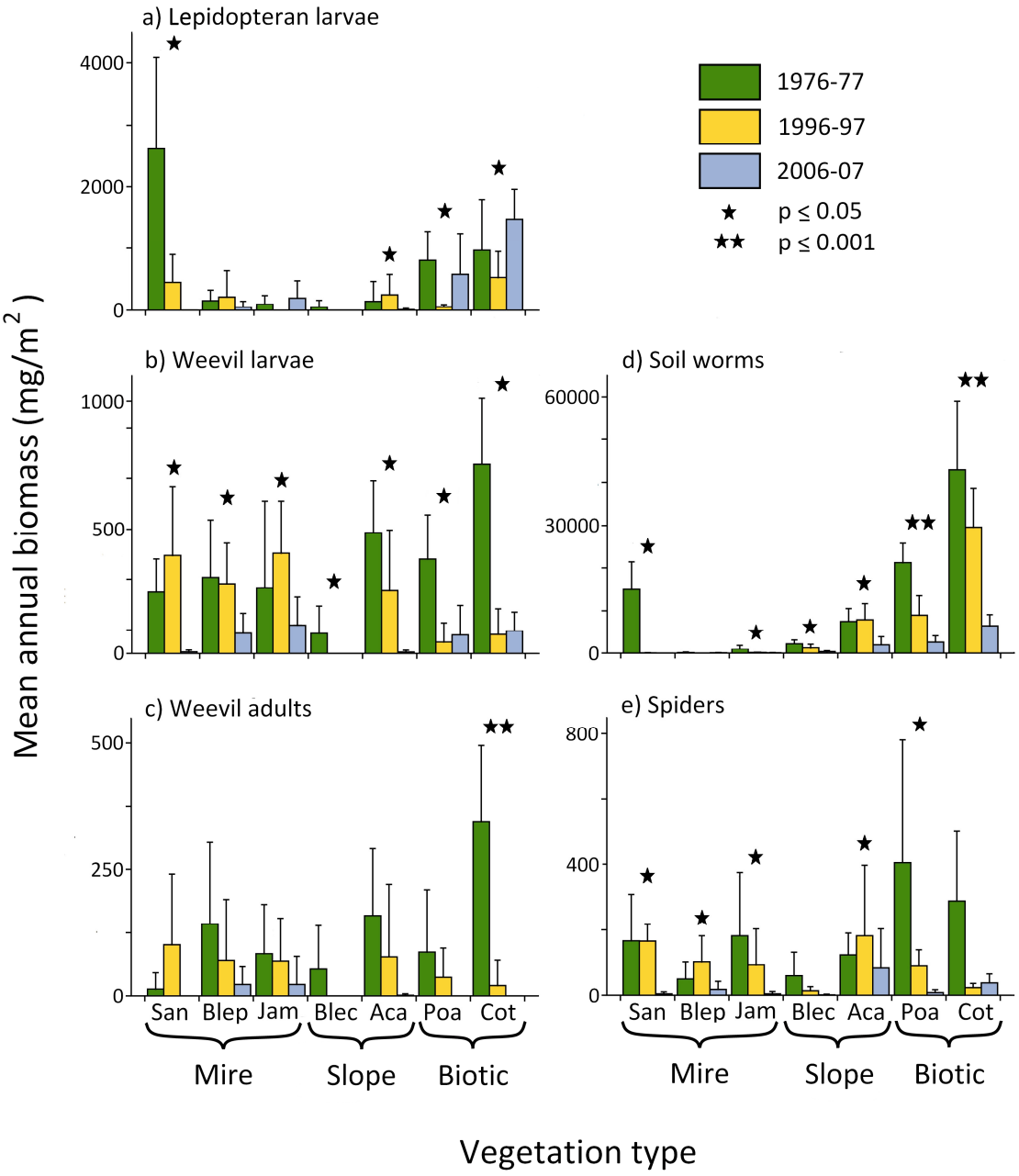


Figure 4

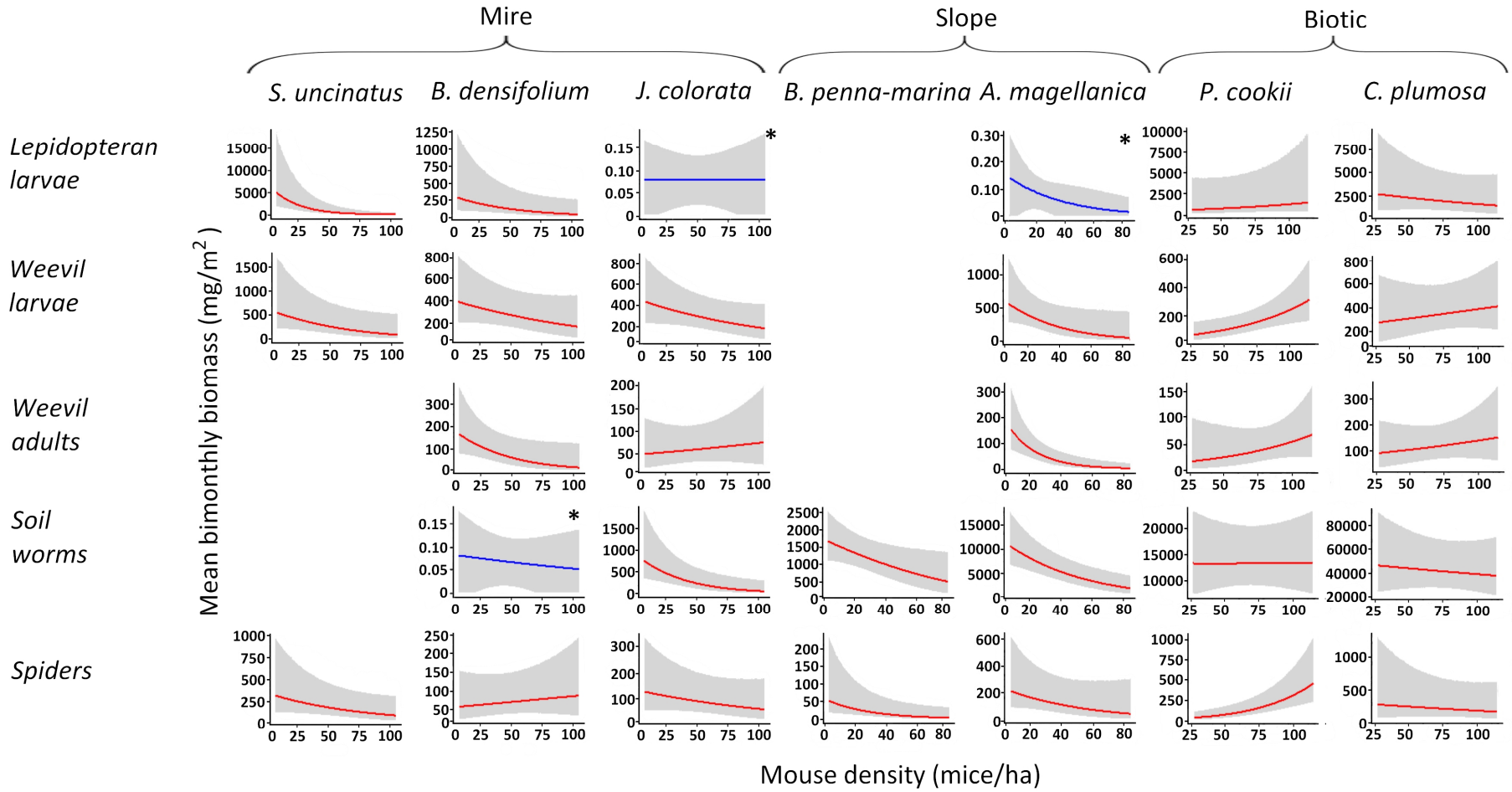


Figure 5

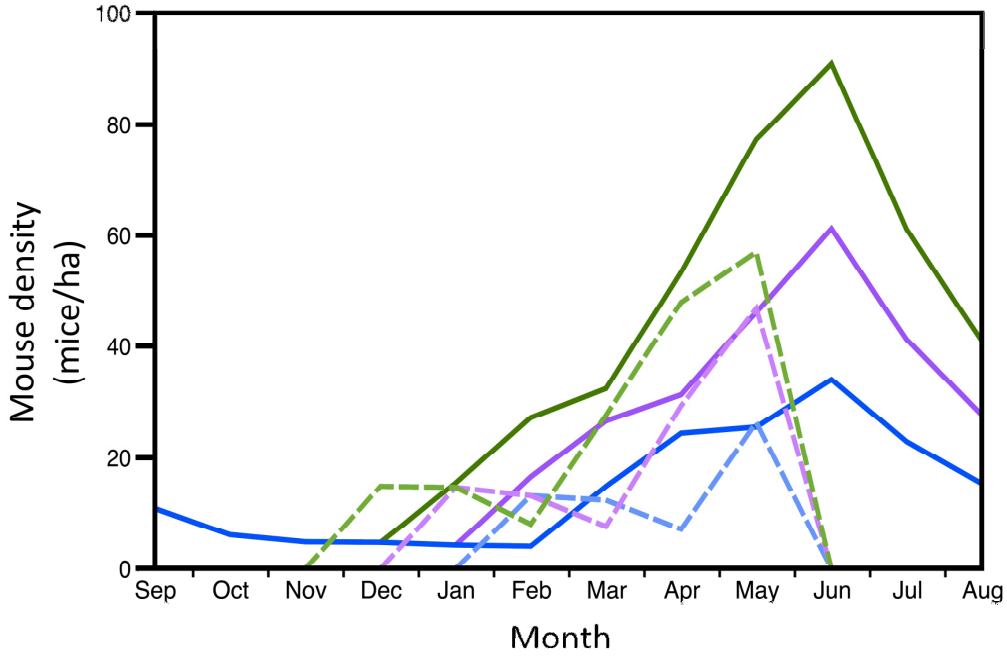


Figure 6

Supplementary Materials

Supplementary Table A1: Density estimates (per hectare) of mice in the mire habitat on Marion Island. Lower and upper 95 % confidence limits are presented in brackets.

	1991-92	1993-94	1996-97	1998-99	2008-09 East	2008-09 West	2009-10 East	2009-10 West	2010-11 East	2010-11 West
Apr				122.9 (91.0,166.1)						
May		64.9 (48.9,86.1)		112.6 (86.3,147.0)			236.6 (158.8,352.5)	164.2 (114.8,234.7)	214.0 (156.8,292.1)	69.0 (35.4,134.7.7)
Jun	27.1 (19.7,37.2)		43.6 (31.0,61.1)	51.6 (38.8,68.7)			79.4 (56.4,111.8)			
Jul		55.0 (37.6,80.2)	25.6 (16.6,39.4)	23.4 (16.7,32.9)				108.9 (80.0,142.7)	134.4 (86.4,209.2)	112.1 (76.6,164.0)
Aug	24.8 (17.2,35.7)	35.5 (18.6,67.8)		17.0 (11.7,24.7)			21.9 (11.7,40.7)			
Sep		59.1 (43.4,80.4)	35.7 (18.7,68.2)	12.9 (8.3,20.0)	14.6 (7.4,29.0)	18.4 (10.5,32.4)		41.6 (26.5,65.2)	51.9 (26.9,100.0)	52.6 (32.5,85.0)
Oct	9.3 (5.2,16.6)	39.4 (29.6,52.5)		15.9 (10.2,24.7)			24.7 (11.4,53.8)		13.7 (7.6,24.6)	
Nov		17.1 (9.6,30.3)	17.9 (11.3,28.2)	24.0 (16.8,34.3)	14.3 (8.6,23.7)	40.8 (20.4,81.4)	4.3 (1.2,15.3)	15.1 (7.6,29.9)		21.6 (11.2,41.6)
Dec	2.5 (0.8,7.4)	15.9 (10.1,25.1)		33.7 (20.3,56.1)					43.9 (22.2,86.8)	
Jan		9.0 (4.8,16.7)	18.3 (8.3,40.6)	44.5 (32.5,60.9)	21.6 (7.9,58.7)	44.6 (31.3,63.7)	15.5 (6.3,37.8)	2.6 (0.7,9.9)		63.1 (31.9,124.7)
Feb	17.8 (11.2,28.4)	22.6 (8.7,58.8)						149.3 (109.3,203.9)	65.7 (20.9,207.0)	
Mar		36.8	50.9	128.5	21.6	176.7	155.6			107.1

	(21.1,64.3)	(23.9,108.5)	(93.3,176.9)	(11.3,41.1)	(113.6,274.9)	(102.7,235.7)	(68.5,167.4)
Apr	51.3 (34.6,81.6)		116.2 (85.3,158.2)				

Supplementary Table A2: Density estimates (per hectare) of mice in the slope habitat on Marion Island. Lower and upper 95 % confidence limits are presented in brackets.

	1991-92	1993-94	1998-99	2008-09	2009-10	2010-11
Apr			49.9 (35.2,70.9)		105.7 (79.1,141.1)	
May	48.0 (36.7,62.8)	44.6 (31.2,63.8)	48.2 (38.0,61.3)			210.1 (160.9,274.3)
Jun	16.5 (11.2,24.4)	28.5 (18.5,43.9)	20.1 (15.1,26.6)		80.1 (52.7,121.9)	
Jul	21.7 (15.1,31.2)	50.3 (33.7,75.2)				22.1 (7.4,65.4)
Aug	8.1 (4.3,15.4)	21.1 (12.2,36.4)	9.2 (5.8,14.6)	42.9 (29.3,62.7)	13.7 (7.0,26.5)	20.6 (13.1,32.4)
Sep	6.5 (3.4,12.4)	35.5 (25.0,50.4)	10.9 (7.8,15.4)			
Oct	0.8 (0.2,2.5)	24.9 (16.4,37.6)	6.1 (3.5,10.7)	7.8 (4.0,15.4)	12.3 (6.0,25.2)	33.0 (19.0,57.3)
Nov	1.1 (0.3,3.0)	18.8 (12.7,27.7)	5.9 (3.4,10.2)			
Dec	2.7 (1.1,6.8)	19.7 (13.9,27.8)	6.3 (3.6,10.8)	7.3 (3.1,17.3)	8.6 (3.5,21.4)	11.9 (3.5,41.4)
Jan	1.3 (0.5,3.2)	10.2 (6.0,17.4)	9.6 (5.4,17.0)			
Feb	5.9 (2.9,11.9)	46.4 (32.5,66.2)	17.7 (12.7,24.7)	37.9 (18.7,77.0)	8.5 (3.2,22.7)	65.8 (34.1,126.9)
Mar	29.9 (14.4,62.5)	27.2 (17.8,41.4)	22.6 (17.7,28.8)		36.0 (23.8,54.5)	
Apr		47.7 (35.3,64.4)	27.3 (19.5,38.1)			

Supplementary Table A3: Density estimates (per hectare) of mice in the biotic habitat on Marion Island. Lower and upper 95 % confidence limits are presented in brackets.

	1991-92	1993-94	1996-97	1998-99	2008-09 East	2008-09 West	2009-10 East	2009-10 West	2010-11 East	2010-11 West
Apr				117.4 (74.3,185.7)			222.2 (181.2-272.5)		132.3 (97.7,180.5)	
May	246.6 (194.0,313.4)	82.3 (60.9,111.3)	142.7 (120.3,169.2)	93.3 (74.0,117.6)				93.4 (63.8,136.6)		109.3 (80.2,149.1)
Jun	54.3 (40.8,72.2)	95.0 (69.1,130.7)		74.1 (55.0,99.9)			50.5 (30.2,84.4)		77.2 (35.5,168.0)	
Jul	33.0 (24.2,45.1)	94.0 (46.7,189.1)	67.0 (52.6,85.3)	34.0 (26.8,43.1)				98.6 (73.4,132.4)		35.8 (20.5,62.5)
Aug	28.1 (20.1,39.2)	80.6 (47.4,137.1)		19.0 (13.8,26.3)	131.7 (77.8,222.9)		20.8 (9.0,48.3)		20.3 (11.5,35.7)	
Sep	29.8 (22.0,40.3)	48.7 (36.2,65.5)	43.2 (32.8,56.8)	11.1 (7.6,16.2)		75.4 (49.8,114.2)		18.5 (10.1,33.9)		45.2 (18.4,116.2)
Oct	40.9 (27.8,60.3)	50.8 (39.4,65.5)		15.1 (10.7,21.5)	65.3 (44.5,95.9)		8.2 (3.4,21.7)		17.2 (6.2,47.3)	
Nov	21.6 (15.4,30.2)	48.5 (36.1,65.1)	41.2 (21.4,79.2)	16.5 (12.4,21.8)		123.1 (53.9,281.2)		27.1 (7.5,97.4)		14.2 (8.2,24.6)
Dec	67.1 (52.1,86.3)	58.5 (38.3,89.4)		67.1 (50.5,89.1)			49.4 (27.0,90.4)		21.7 (11.4,41.3)	
Jan	39.1 (29.9,51.2)	41.3 (28.7,59.4)	21.8 (12.5,37.8)		120.9 (87.4,167.1)	198.1 (150.9,260.2)		60.8 (32.9,112.4)		121.8 (59.4,249.9)
Feb	90.1 (64.7,125.5)	123.9 (94.7,162.1)		95.3 (78.7,115.4)			32.0 (14.7,69.5)		51.0 (32.3,80.6)	
Mar	103.3 (87.8,121.4)	122.7 (97.8,151.5)	80.2 (52.6,122.3)	102.1 (84.2,123.9)	115.4 (85.5,165.5)	172.9 (142.1,210.4)		226.1 (175.9,290.6)		160.5 (129.1,199.5)
Apr		134.1 (91.7,196.1)	102.2 (67.2,155.7)	72.5 (57.9,90.8)						

Supplementary Table A4: Summary of model selection for mouse survival in three habitat types on Marion Island. Additive effects are denoted by '+', interactive effects by '*'. Model selection was based on Akaike's Information Criterion adjusted for overdispersion and sample size (QAICc), where a smaller value indicates a better model. ΔQAICc is the difference in QAICc between the current model and the best. QAICc weights give the relative support each model has compared to the others, and K is the number of parameters. QDeviance is the model deviance divided by the variance inflation factor ĉ. Models with ΔQAICc > 7 only are shown.

		Model	QAICc	ΔQAICc	QAICc weights	K	QDeviance
Mire	1991-92	Age + Precipitation	109.243	0.000	0.681	4	100.835
		Age * Month	112.150	2.908	0.159	6	99.275
		Age + Month	112.163	2.920	0.158	6	99.288
	1993-94	Month	875.751	0.000	0.244	13	849.051
		Age + Month	875.956	0.184	0.222	14	847.126
		Invertebrate density	876.190	0.438	0.196	4	868.114
		Age + Invertebrate density	876.644	0.892	0.156	5	866.530
		Age * Invertebrate density	877.543	1.791	0.100	6	865.383
		Age + Mouse density	880.344	4.593	0.024	6	870.230
		Age * Month	882.116	6.365	0.010	18	844.788
		Age + Temperature	882.163	6.411	0.010	5	872.049
		Age * Mouse density	882.382	6.631	0.009	6	870.223
	1996-97	Age + Precipitation	359.757	0.000	0.421	5	349.548
		Trapping grid + Age + Precipitation	361.616	1.859	0.166	6	349.323
		Age + Temperature	362.826	3.069	0.091	5	352.617
		Trapping grid * Age + Precipitation	363.682	3.924	0.059	7	349.289
		Trapping grid + Age + Temperature	364.645	4.888	0.037	6	352.351
		Age + Month	364.670	4.913	0.036	8	348.163
		Trapping grid + Age	364.677	4.920	0.036	5	354.467
		Trapping grid + Age + Invertebrate density	365.260	5.503	0.027	6	352.966
		Trapping grid + Age * Precipitation	366.303	6.545	0.016	7	347.667
	1998-99	Trapping grid * Age + Month	1219.726	0.000	0.732	15	1189.099
		Trapping grid * Age + Invertebrate density	1224.009	4.283	0.086	7	1209.864
		Trapping grid + Age + Month	1224.237	4.511	0.077	14	1195.689
		Trapping grid + Age * Invertebrate density	1226.332	6.606	0.027	9	1208.099
Slope	1991-92	Invertebrate density	110.619	0.000	0.527	3	104.475

		Mouse density	112.650	2.031	0.191	3	106.506
		Month	113.972	3.354	0.099	9	94.855
		Precipitation	114.426	3.807	0.079	3	108.282
		Temperature	115.448	4.829	0.047	3	109.304
	1993-94	Age * Month	1985.320	1.000	1.000	17	1949.9414
	1998-99	Trapping grid *Age* Temperature	820.787	0.000	0.765	13	794.153
		Trapping grid * Temperature	824.227	3.440	0.137	8	807.979
		Trapping grid + Age * Temperature	825.178	4.391	0.085	12	800.635
Biotic	1991-92	Age + Mouse density	904.388	0.000	0.663	5	894.298
		Age * Mouse density	906.359	1.971	0.248	6	894.233
		Age + Month	909.644	5.256	0.048	13	883.089
		Age * Month	910.010	5.622	0.040	16	877.177
	1993-94	Age + Invertebrate density	833.587	0.000	0.538	5	823.515
		Age * Invertebrate density	835.224	1.638	0.237	6	823.123
		Age	838.028	4.441	0.058	4	829.980
		Age * Mouse density	838.382	4.796	0.049	6	826.281
		Age + Precipitation	839.306	5.720	0.031	5	829.234
		Age + Temperature	839.725	6.139	0.025	5	829.654
		Age + Mouse density	840.050	6.463	0.021	5	829.978
	1996-97	Trapping grid + Age * Month	2058.070	0.000	1.000	17	2022.945
	1998-97	Age + Temperature	937.375	0.000	0.477	5	927.329
		Trapping grid + Age + Temperature	938.951	1.5756	0.217	7	924.864
		Age + Invertebrate density	940.531	3.1553	0.098	5	930.484
		Trapping grid + Temperature	941.879	4.504	0.050	6	929.814
		Trapping grid * Age + Temperature	941.931	4.556	0.047	9	923.791
		Trapping grid + Age + Invertebrate density	942.218	4.842	0.042	7	928.130
		Trapping grid + Invertebrate density	943.749	6.374	0.042	7	928.130
		Trapping grid + Age + Temperature	944.087	6.714	0.017	12	919.845

Supplementary Table A5: Estimated impact of earlier breeding in the Marion Island mouse population based on the matrix population model. The start of the breeding season refers to the first appearance of juvenile mice in traps. All values refer to mice·ha^{-1}.

Start of Breeding Season	Age Class	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug
February	Juvenile	0	0	0	0	0	13.2	12.4	7.2	26.3	0	0	0
	Subadult	0	0	0	0	0	0	11.1	10.4	4.8	14.3	0	0
	Adult	10.9	6.2	4.9	4.9	4.3	4.1	3.8	14	20.7	19.7	22.9	15.4
	Total	10.9	6.2	4.9	4.8	4.3	17.3	27.3	31.6	51.8	34.0	22.9	15.4
January	Juvenile	0	0	0	0	14.7	13.2	7.7	29.3	46.9	0	0	0
	Subadult	0	0	0	0	0	12.5	11.1	6.4	19.5	25.5	0	0
	Adult	10.9	6.2	4.9	4.8	4.3	4.1	15.5	24.9	26.7	35.7	41.2	27.7
	Total	10.9	6.2	4.9	4.8	19.0	29.8	34.3	60.6	93.1	61.2	41.2	27.7
December	Juvenile	0	0	0	14.9	14.7	8.1	27.6	48.0	57.0	0	0	0
	Subadult	0	0	0	0	11.2	12.5	6.9	23.1	31.9	31.0	0	0
	Adult	10.9	6.2	4.9	4.8	4.3	14.7	25.5	30.3	45.4	59.9	61.1	41.0
	Total	10.9	6.2	4.9	19.7	30.2	35.3	60.0	101.4	134.3	90.9	61.1	41.0

Supplementary Table A6: Annual mean biomass (dried mg m^{-2}) (± SE) of macro-invertebrates found in the major vegetation complexes at Marion Island, 1976-77, 1996-1997, and 2006-07. Kruskal Wallis tests were used to test for differences between the three study periods. *n* = 90 for all vegetation except *S. uncinatus* which is *n* = 80.

Habitat	Vegetation	Invertebrate Group	1976-77	1996-97	2006-07	χ^2	*p*
Mire	*S. uncinatus*	Lepidopteran larvae	2 616.1 (±) 1 470.1	443.3 (±) 452.6	0	11.96	0.003
		Weevil adults	13.3 (±) 32.5	100.9 (±) 139.8	0	3.46	ns
		Weevil larvae	245.4 (±) 129.9	389.2 (±) 272.3	6.1 (±) 7.6	7.87	0.020
		Soil worms	15 053.4 (±) 6 376.8	25.4 (±) 62.3	0	12.95	0.002
		Spiders	165.8 (±) 142.7	165.1 (±) 51.8	4.3 (±) 6.1	10.76	0.005
	B. densifolium	Lepidopteran larvae	142.6 (±) 173.2	204.0 (±) 429.7	41.8 (±) 91.2	1.12	ns
		Weevil adults	142.6 (±) 160.4	69.7 (±) 121.2	22.5 (±) 35.4	3.46	ns
		Weevil larvae	301.7 (±) 229.1	276.4 (±) 162.0	80.5 (±) 79.7	6.88	0.032
		Soil worms	102.8 (±) 147.5	0	54.5 (±) 60.9	4.14	ns
		Spiders	49.7 (±) 51.5	101.5 (±) 79.9	17.7 (±) 24.8	11.61	0.003
	J. colorata	Lepidopteran larvae	99.5 (±) 127.7	0	179.1 (±) 306.9	5.19	ns
		Weevil adults	82.9 (±) 97.8	66.7 (±) 85.2	22.6 (±) 55.4	1.65	ns
		Weevil larvae	261.9 (±) 344.0	398.4 (±) 213.7	113.4 (±) 114.6	6.66	0.036
		Soil worms	855.5 (±) 922.8	72.2 (±) 109.3	49.1 (±) 76.6	11.16	0.004
		Spiders	149.2 (±) 192.4	92.8 (±) 110.4	5.1 (±) 10.0	12.23	0.002
Slope	*B. penna-marina*	Lepidopteran larvae	43.1 (±) 105.6	0	0	2.00	ns
		Weevil adults	53.1 (±) 86.0	0	0	4.24	ns
		Weevil larvae	79.6 (±) 109.7	0	0	6.73	0.035
		Soil worms	2 132.0 (±) 936.0	1 201.1 (±) 855.9	354.0 (±) 211.1	10.26	0.006
		Spiders	59.7 (±) 71.2	13.6 (±) 12.6	1.2 (±) 2.1	5.23	ns
	A. magellanica	Lepidopteran larvae	132.6 (±) 324.9	240.4 (±) 332.0	0.7 (±) 1.6	6.60	0.037
		Weevil adults	159.2 (±) 131.4	76.7 (±) 143.9	1.2 (±) 3.0	3.92	ns
		Weevil larvae	480.8 (±) 203.8	251.0 (±) 240.0	5.5 (±) 7.7	12.64	0.002
		Soil worms	7 477.0 (±) 3 063.8	7 894.4 (±) 3 798.5	1 902.4 (±) 1 929.3	9.03	0.011
		Spiders	122.7 (±) 67.1	181.3 (±) 215.4	83.4 (±) 119.6	11.03	0.004
Biotic	*P. cookii*	Lepidopteran larvae	802.4 (±) 471.9	47.1 (±) 33.4	574.2 (±) 666.5	7.94	0.019
		Weevil adults	86.2 (±) 123.7	36.8 (±) 57.5	0	3.73	ns

	Weevil larvae	374.7	(±)	175.9	44.8	(±)	77.2	73.3	(±)	118.7	9.92	0.007
	Soil worms	21 233.9	(±)	4 563.2	8 956.9	(±)	4 622.0	2 556.7	(±)	1 496.3	14.75	<0.001
	Spiders	404.5	(±)	375.9	89.6	(±)	48.7	8.0	(±)	8.8	11.06	0.004
C. plumosa	Lepidopteran larvae	964.9	(±)	825.6	520.9	(±)	425.1	1 473.7	(±)	483.7	6.23	0.044
	Weevil adults	344.8	(±)	150.3	20.4	(±)	49.9	0			14.84	<0.001
	Weevil larvae	749.4	(±)	262.3	75.6	(±)	102.9	90.5	(±)	74.5	11.62	0.003
	Soil worms	42 912.2	(±)	16 086.0	29 611.5	(±)	9 012.5	6 447.6	(±)	2 635.1	13.05	<0.001
	Spiders	288.5	(±)	211.2	23.2	(±)	12.9	37.8	(±)	27.5	1.73	ns

Chapter 3 – Black-faced sheathbill ecology in response to ecosystem change

"This bird is common on both the Prince Edward Islands and Kerguelen's Land, and is called 'wide-awake' by the sealers. When Mr. Harris first landed, the birds were so tame that he frequently had to kick them out of his way; and when he hid himself behind the rocks, they would come and peep over at him, chattering, and seemingly quite pleased that they had found him " **– F.W. Hutton, 1865**

Black-faced sheathbill (*Chionis minor marionensis*),
with metal and darvic rings, Marion Island

Introduction

Islands are important sources of global diversity (Myers et al., 2000; Kier et al., 2009). Though generally low in species richness relative to continental regions (MacArthur and Wilson, 1967; Carlquist, 1974), under sufficient geographic and temporal isolation and often unconstrained by the evolutionary pressures found on continents, high levels of endemism can occur (Grant, 1998; Schluter, 2000). Consequently, islands contain a disproportionate percentage of global terrestrial floral (25 %; Kreft et al., 2008), avian (17 %; Newton and Dale, 2001), mammalian (14 %; Alcover et al., 1998), and reptilian (12 %; http://www.reptile-database.org) diversity, despite representing only 3.6 % of the terrestrial surface of the world. Unfortunately, many of the same forces that promote endemnicity also leave insular biota remarkably vulnerable to rapid ecosystem change (Sadler, 1996; Cronk, 1997). In consequence, most of the world's contemporary extinctions have occurred on islands (Honegger, 1981; Alcover et al., 1998; Szabo et al., 2012) and they remain the site of most threatened species (Vié et al., 2008).

The high rate of extinctions on islands is causally linked to the direct and indirect effects of human colonization and visitation (Diamond, 1989; Blackburn and Gaston, 2005; Whittaker and Fernández-Palacios, 2007). Whereas human hunting has been ascribed to a significant proportion of historical extinctions (Steadman, 1995; Duncan and Blackburn, 2004; Loehle and Eschenbach, 2012), alien species, alongside direct habitat alteration on inhabited islands, pose the most significant contemporary threats to insular biota (Clout and Veitch, 2002; Courchamp et al., 2003; Clavero et al., 2009).

Alien species cause native species losses primarily through direct predation (Atkinson, 1985; Savidge, 1987; Holdaway, 1999; Courchamp et al., 2003; Blackburn et al., 2004; Duncan and Blackburn, 2004, 2007; Towns et al., 2006; Wanless et al., 2007; Jones et al., 2008) and habitat transformation through herbivory (Coblentz, 1978; King, 1985; Morin and Conant, 1998; Donlan et al., 2002; Bergstrom et al., 2009; Brodier et al., 2011) but also indirectly by acting as vectors of disease (van Riper, 1991; Wikelski et al., 2004; Carrete et al., 2009), mutualism disruption (Lammers and Freeman 1986; Robertson *et al.* 1999; Delgado García 2002), trophic cascades (Schoener and Spiller 1999; O'Dowd et al. 2003; Kurle et al. 2008), and exploitative competition with native species (Case, 1996; Hansen et al., 2002; Harris and Macdonald, 2007; Ruffino et al., 2008; Milazzo et al., 2013).

Increasingly, another threat in the form of global climate change must also be considered as the pervasive effects of a changing climate are likely to have far-reaching consequences for many island systems. How climate change will impact insular biota is poorly understood, though it has been suggested that island populations are disproportionately vulnerable (Fordham and Brook, 2008). While continental populations may adapt to climate change through dispersal, terrestrial island endemics must adapt to a changing environment through either phenotypic plasticity or evolution (Gienapp et al., 2008; Gilman et al., 2010), which are processes potentially inhibited by decreased genetic variability (Frankham, 1995; Fordham and Brook, 2008). Further, given that most of the world's islands are under some form of anthropogenic disturbance (Clark and Dingwal, 1985), climate change is likely to interact with multiple global change drivers. For alien species, such interactions are likely to be additive, if not synergistic, as warming climates are largely forecast to increase both the rate and range of colonization and the impacts of already established species (Cannon, 1998; Dukes and Mooney, 1999; Hellmann et al., 2008; Tylianakis et al., 2008; Walther et al., 2009 but see Darling and Côté, 2008).

A significant effect of climate change may be realized by altering interspecific interactions (Walther et al., 2002), specifically food webs (Petchey et al., 1999; Zarnetske et al., 2012; Cahill et al., 2013). For islands, such interactions are often simpler and thus more prone to disturbance (Elton, 1958; Holt, 1996; Takimoto et al., 2008). Further, the strongest effects of these changes are expected when species lack a coevolutionary history with each other (Urban et al., 2012). Under such scenarios not only the direct but also the indirect effects of alien species may rise in prominence. For example, on more temperate islands, competition is expected to enhance extinction risk as warmer adapted competitors gain an increasing advantage (Norberg et al., 2012; Urban et al., 2012). Thus climate change has the potential to affect insular biota on several fronts, independently and in synergy with other global change drivers. The full suite of potential biological interactions under such scenarios makes predicting outcomes difficult. Nevertheless, the outcomes of these interactions have important implications for populations, community structure, and ecosystem functioning (Tylianakis et al., 2007; Harmon et al., 2009; Norberg et al., 2012). Understanding the full complexity of species response to these higher order effects is therefore vital for better prediction and management of island species declines (Didham et al., 2005; Brook et al., 2008).

The black-faced sheathbill (*Chionis minor marionensis* Reichenow; hereafter sheathbill) of sub-Antarctic Marion Island provides an ideal opportunity to investigate the extent to which climate change and alien species interact to have population-level effects on insular biota.. Marion Island has experienced rapid warming and drying over the past few decades (le Roux and McGeoch, 2008a). Sheathbills are terrestrial endemic shorebirds that forage in penguin colonies in the breeding season, with a significant proportion of the population switching to terrestrial invertebrates in winter after many penguins have left the island (Burger, 1981a). The winter foraging ecology of sheathbills markedly changed between the 1970s and 1990s, possibly due to exploitative competition with invasive house mice (*Mus musculus* Linnaeus) for terrestrial invertebrate prey (Huyser et al., 2000). Further, rockhopper penguins (*Eudyptes chrysocome filholi* Hutton), an important foraging resource for breeding sheathbills, are in significant long-term decline (Crawford et al., 2009), possibly driven by climate change (Cunningham and Moors, 1994; Crawford et al., 2003; Crawford, et al., 2008; Dehnhard et al., 2013). Short-term data suggests that such changes to the sheathbill environment have led to a population decline (Huyser et al., 2000), but demographic analysis is lacking and the status of the population unknown. Here I test the hypothesis that the Marion Island sheathbill population is in decline and examine the changes in ecology possibly responsible. In particular, I determine whether the changes in sheathbill foraging behaviour first observed by Huyser et al. (2000) have continued and whether these changes can be associated with a climate-driven increase in competition with invasive mice. I then examine how these changes have affected sheathbill demography, including body condition, breeding, and sex ratio. Finally, I examine if these demographic changes, in addition to differing population trends within different penguin species, have created a source-sink metapopulation dynamic between sheathbills that use different habitats, and its potential long-term consequences.

Methods

Study area and species

The sub-Antarctic Prince Edward Island group is comprised of larger Marion Island (46°54'S, 37°45'E) (hereafter MI) and smaller Prince Edward Island (46°37'S, 37°55'E) (hereafter PEI). The islands are volcanic in origin and located approximately 2100 km southeast of Cape Town, South Africa. Nineteen km separate the islands at their closest point. The islands have

a hyperoceanic climate (mean annual temperature c. 6.5°C, total precipitation of c. 1900 mm), but are currently experiencing rapid climate change. Since the late 1970s, when the effects of global dimming ceased counterbalancing rising temperatures (Hansen et al., 2006), mean annual temperature has increased by approximately 1.8° C (le Roux and McGeoch, 2008b) and the number of frost days has significantly declined (Huyser et al., 2000). Over the same period precipitation has declined by 20% and the duration of dry spells has increased (le Roux and McGeoch, 2008a), leading to a significant reduction in peat moisture content (Chown and Smith, 1993).

The Prince Edward Islands are characterised by two biomes; polar desert above 650 m a.s.l., and sub-Antarctic tundra below (Chown and Froneman, 2008). Five habitat complexes comprise the sub-Antarctic tundra biome; mire (wet peaty areas), slope (lowland areas with well-drained slopes), biotic (areas manured by seals and seabirds), saltspray (highly saline coastal herbfield), and fellfield (vascular plant cover dominated by cushions of *Azorella selago*).

The islands share most of their indigenous species and are relatively depauparate in plant and invertebrate species richness (Chown and Froneman, 2008). However, they are internationally-important breeding sites for a number of seabirds and seals. Twenty-nine seabird species breed or are suspected to breed between the two islands including four species of penguin, five species of albatross, and 15 species of petrel (Cooper and Brown, 1990; McClelland et al., 2013). Marion Island is especially important for penguins and supports 13 % of the global king penguin (*Aptenodytes patagonicus* Miller) population, 80 % of which is divided between two colonies at King Penguin and Kildalkey bays (Crawford and Cooper, 2003). The population of the eastern race of southern rockhopper penguin is 17 % of the world population (Ryan and Bester, 2008). Southern elephant seal (*Mirounga leonin*a Linnaeus), Antarctic fur seal (*Arctocephalus gazella* Peters), and 33 % of the global Sub-Antarctic fur seal (*Arctocephalus tropicalis* Gray) population are also present on the islands (Hofmeyr et al., 2006). Sheathbills are the lone indigenous terrestrial vertebrate.

Marion Island has far more invasive species than Prince Edward Island (Chown and Froneman, 2008). The now exterminated domestic cat (*Felis cattus* Linnaeus) was present from 1949-1991, over which time it was responsible for a significant decline in the Marion Island petrel fauna (van Rensburg and Bester, 1988). House mice were introduced to the

island sometime after 1818 (Watkins and Cooper, 1986), continue to persist, and have greatly reduced the biomass of terrestrial invertebrates (Chown and Smith, 1993; Chapter 2). In consequence, Prince Edward Island has significantly higher petrel and terrestrial invertebrate densities than Marion Island (Schramm, 1986; Crafford and Scholtz, 1987). A comprehensive overview of the biology, geology, and climate of the Prince Edward Islands is provided by Chown and Froneman (2008).

Sheathbills are sexually dimorphic (the male is 10 % to 15 % larger) long-lived (up to at least 24 years; McClelland and Chown unpublished data) monogamous shorebirds. Movement of sheathbills between PEI and Marion Island has yet to be recorded and the two populations are likely closed to immigration and emigration. Sheathbills are generally free of predation pressure. Whilst brown skuas (*Catharacta antarctica lonnbergi* Mathews) occasionally pursue sheathbills, kills are infrequent (Burger, 1982) and increasingly so on Marion Island where skuas are rapidly declining (Ryan et al., 2009). In some respects the Marion Island sheathbill population can be considered two sympatric groups. The first group (hereafter KP sheathbills) forages year-round in continuously-occupied king penguin colonies where they consume mostly the stomach contents of penguins obtained through kleptoparasitism, penguin carcasses, and excreta (Burger, 1984). The second group (hereafter RH sheathbills) occupies eastern rockhopper penguin colonies during their breeding season and their diet is similar to that of KP sheathbills during this period (Burger 1981b; Burger 1984). However, when rockhopper penguins leave the island after their five-month breeding season, RH sheathbills switch to either marine or terrestrial invertebrates for the remainder of the year. For both sheathbill groups, breeding pairs unable to secure a territory will not breed and the number of breeding territories within penguin colonies is considered the limiting factor regulating population growth (Burger, 1979). A large macaroni penguin (*Eudyptes chrysolophus* Brandt) population (*c*. 290 000 breeding pairs) is also present on Marion Island, with most birds breeding in one of two large colonies (Crawford et al., 2009). These colonies contain few suitable nesting sites for sheathbills and exceptional penguin densities limit sheathbill movement within them, rendering these areas of little value to sheathbill breeding (Burger, 1979).

The Marion Island black-faced sheathbill population was previously studied from 1974-78 (Burger, 1979, 1981a), and from 1994-95 (Huyser et al., 2000). Both studies were limited to a small portion of the eastern side of the island and focused primarily on foraging

ecology. Between 1976-77 and 1994-95 the number and proportion of sheathbills foraging inland for terrestrial invertebrates declined significantly (Huyser et al., 2000). A corresponding decline in sheathbill body mass and clutch size was also reported, though limited population surveys and a lack of demographic analysis left population trends largely unknown.

For this study, sheathbills were studied in three areas on Marion Island from May 2008 to March 2011 (Fig. 1). The east study area matched that used in previous studies and consisted of 6.5 km of coastline from the weather station to East Cape. Additional study areas were added to the north (3.6 km, Storm Petrel Bay to Log Beach) and west (6.8 km, Mixed Pickle Cove to Chess Castle Beach) portions of the island for a better understanding of whole-island sheathbill ecology. The east study area was characterized by one large king penguin colony (*c.* 940 breeding pairs; Archway Bay) and several large beaches. The north study area contained one king penguin colony (*c*. 1 500 breeding pairs; Log Beach), steep cliffs, and very few beaches. The western study area did not contain a king penguin colony but contained by a considerable degree the largest rockhopper penguin population (Crawford et al., 2003), intertidal zone, and approximately half of the island's sub-Antarctic fur seal population (Hofmeyr et al., 2006).

Capture and morphometrics

A total of 1381 sheathbills were captured by hand with a hoop net or foot hook. All birds were given a numbered stainless steel ring on one leg and a numbered darvic colour ring on the other. Measurements taken included body mass (measured to the nearest 5 g with a 1000-g Pesola scale; Baar, Zug, Switzerland), culmen length (exposed culmen to tip of bill), and culmen depth (highest point of the sheath to the under edge of the lower mandible), culmen width (taken at the nostrils). Birds were sexed and aged following Burger (1980). Sex was determined by mate comparison (where the largest bird was assumed male) or beak shape index (BSI; $\frac{culmen\ length * culmen\ width * culmen\ depth}{10}$), where BSI scores above 450 were assumed male. Birds were aged (juvenile; 1 yr-olds, subadult; 2 and 3 yr-olds, and adult; ≥ 4 yr-olds) in the absence of breeding behaviour by facial features.

Foraging/count surveys

Foraging/count surveys were conducted within each study area from May 2008 to March 2011 at 14-day intervals with methodology following Burger (1981). Counts were conducted on foot with binoculars along the coast, but regular scans were made of inland areas up to 200 m from shore. Counts were conducted in daylight hours but start time and at which end of the study area the survey started varied to limit any diurnal bias in behaviour and habitat use. Sheathbills are curious and approachable so observers wore natural-toned clothing to limit attracting birds or altering their behaviour. Recorded for each bird when encountered was the presence of a ring, ring number, geographic coordinates, the habitat in which the bird was first sighted, and if the bird was foraging as a member of a flock. Foraging habitats included the intertidal zone, king penguin colonies, rockhopper penguin colonies, and four vegetation complexes; salt-spray, slope, mire, and biotic. All three study areas contained between one and three small (> 500 breeding pairs) macaroni penguin colonies. For simplicity, sheathbills within these colonies were considered as foraging in rockhopper colonies as the same birds made use of both resources. Biotic sites were further classified to include the marine species (albatross, penguin, fur seal, etc.) likely responsible for manuring whenever possible. Birds that were encountered bathing, in flight, in the base area, and in loafing crèches were included in population counts but removed from foraging analyses. Incubating or brooding birds were assigned to the foraging habitat of their mate. Survey duration, sea height, wind speed, temperature, and precipitation were recorded for all surveys.

Whole-island winter (August/September) surveys of sheathbills were conducted over the course of seven to ten days in 2008, 2009, 2010, and 2011. Surveys were conducted by between two and four independent observers within no more than two weeks of one another. Methods followed those of the fortnightly study area surveys. As sheathbills can be difficult to age by external features alone (Burger, 1980), especially in the absence of close examination, counts estimated absolute population size and did not differentiate between age classes.

Single classification analysis of variance (ANOVA) and Tukey's honestly significant difference tests (Tukey's hsd; $\alpha < 0.05$) were used to test for differences between the three sheathbill study periods (1976-77, 1994-95, and 2008-11) in terms of the total number of sheathbills, and the number of sheathbills in each habitat in the east study area. Each season (winter; May to October, summer; November to April) was analyzed separately. The three

study periods differed in their classification of vegetation habitats. Therefore, to test for differences between the three study periods the four vegetation habitats (biotic, saltspray, mire, and slope) were combined into a single habitat (coastal and inland vegetation) for analyses. However, a comparison using the four separate vegetation habitats was possible between 1976-77 and 2008-11 data and used two-sample *t*-tests. To compare the proportion of sheathbills foraging in each habitat in each season the data were logit-transformed prior to analysis following Warton and Hui (2011). Shapiro-Wilk Normality Tests rejected the assumption of normal distribution in one-half of transformed datasets (Supplementary Table A1). Mann-Whitney-Wilcoxon (MWW) tests for nonparametric data were therefore used after confirming no meaningful difference between *t*-tests and MWW tests for the parametric datasets (Supplementary Table A2:A3). Analyses were performed in the statistical software R 2.15.0 (R Development Core Team, 2010).

Energetics

To explore possible links between changes in sheathbill winter foraging behaviour and changes to the Marion Island environment, the caloric energy in the form of macro-invertebrate prey, currently and historically available on Marion Island was first estimated. As 85 % of all sheathbills foraging for invertebrates traditionally did so in the mire and biotic vegetation (Burger, 1982), the analysis focused on these two habitats. For each habitat the mean winter biomass of the five main prey groups upon which sheathbills forage (soil annelid worms, lepidopteron larvae, weevil adults, weevil larvae, and spiders; Chapter 2) was taken and multiplied by its caloric value (Burger, 1978). Sampled years were 1976-77, 1996-97, and 2006-07.

The total standing crop of invertebrates in each habitat will not be available to sheathbills because of competition with invasive mice, which have been and remain primarily consumers of invertebrates (Gleeson and van Rensburg, 1982; Chown and Smith, 1993; Smith et al., 2002; Chapter 2). Therefore, to better estimate the amount of energy in the form of invertebrate prey available to foraging sheathbills the amount removed by invasive mice was also estimated. The mean winter density of mice in each habitat in 1979-80, 1992-93, and 2008-11 (Chapter 2) was multiplied by the estimated energy requirements of Marion Island mice (Rowe-Rowe et al., 1989, adjusted by a more accurate estimate of mouse energy assimilation; Johnson et al., 2001). Changes in mouse body mass and diet

composition for each time period (Gleeson and Van Rensburg, 1982; Smith et al., 2002, Chapter 2) were accounted for. It must be noted that mouse density estimates for 1979-80 were based on a modified Petersen Index and are likely an overestimate of true density, whereas estimates from 2008-11 were based on spatially explicit capture recapture methods and likely unbiased (Efford et al., 2004).

Next, the energy requirements of RH sheathbills during the winter season were estimated. Field metabolic rate (FMR) includes the basal rate of metabolism (BMR), and the energetic costs of thermoregulation, locomotion, foraging, digestion, growth, reproduction, as well as all energy expenditures that eventually end up as heat production (Nagy, 1987). The FMR of sheathbills has yet to be directly measured, but several bioenergetic models exist to estimate FMR for birds, among which allometric equations and time-energy-budget analysis are the most common and straightforward (Fort et al., 2011). Considering that most allometric equations are based on the FMR of breeding birds (Nagy et al., 1999), a time-energy-budget analysis was chosen for wintering sheathbills. Time-energy-budget analysis integrates the time an animal devotes to different activities and the energy expenditures associated with each activity, often expressed as a multiple of BMR. The analysis used time activity data collected from wintering RH sheathbills when the population still foraged primarily for invertebrates (Burger, 1982), the mean BMR observed for RH sheathbills (Chapter 4), and the expense of each activity as estimated by Burger (1981b), with the exception of thermoregulation which was recalculated to reflect changes in sheathbill body mass. Sexes were pooled considering male and female sheathbills do not significantly differ in BMR (Chapter 4) or foraging activity (Burger, 1982).

Body mass

Long-term changes in sheathbill body mass were tested for each season (early summer; November to January, late summer; February to April, early winter; May to July, and late winter; August to October). RH and KP sheathbills were analysed separately and analysis was limited to confirmed breeders in the east study area to minimize bias. The breeding habitat of individual sheathbills in 1994-95 could not be determined. However, as the majority of measured birds were taken outside of the king penguin colonies (O. Huyser personal communication), all birds from that year were considered RH sheathbills. As measurements in 1994-95 were limited to early summer, an ANOVA and Tukey's hsd test ($\alpha < 0.05$) was

used for comparisons that included all three study periods. All other comparisons used a two-sample *t*-test.

Breeding biology

Sheathbills nest in rock crevices and earthen burrows of varying degrees of accessibility. Attempts were made to locate all active nests in each study area. However some areas in the west study area could not be monitored due to high rockhopper penguin densities. Occupied nests were checked at 7-day intervals between December 1 and March 1. For each nest in which the nest bowl was accessible I recorded clutch size and measured eggs in 2008-09 and 2009-11. Chicks were not handled during the 14-day brooding stage when chick mortality is highest (Burger, 1979). Chicks were monitored until fledge and measurements taken *ad hoc* once chicks became mobile because of their ability to hide in inaccessible crevices when disturbed.

Sex ratios

Sex ratio is an important demographic parameter, especially in monogamous species (Bessa-Gomes et al., 2004). Population studies that fail to account for adult sex ratio (ASR) may systematically over- or underestimate the reproductive population size if the sex ratio is skewed (Newson et al., 2005). Further, there is often a correlation between the ASR and population trends and habitat quality and thus may be an indicator of a species conservation trend or conservation status (Donald, 2007). Similarly, changes in primary (at lay), secondary (at hatch) and tertiary (at fledge) sex ratios have been reported in several bird species in response to changes in habitat quality (Wegge, 1980; Williams et al., 1993; Komdeur et al., 1997). Sex allocation theory predicts that if prevailing ecological or social circumstances differentially influence the fitness benefits of offspring of each sex, parents should adjust their production to maximize their own fitness (Trivers and Willard, 1973). In size-dimorphic birds such as sheathbills, the larger sex is more "costly" to raise and can have a higher mortality during the nestling period. Therefore, in these species, females in poor condition may skew the brood sex ratio in favour of the less expensive sex.

Adult sex ratio was measured as the ratio of sexually mature (post-third year) males to females ringed in the three study areas. As sheathbills have stable pair bonds, are not known to skip a breeding season, and both sexes share maturation, reproductive, and

survival rates, the ASR was considered synonymous with operational sex ratio (OSR), the ratio of male to female individuals that are ''ready to mate'' at a given time (Emlen and Oring, 1977; Clutton-Brock and Parker, 1992).

Sheathbills cannot be accurately sexed by external measurements until they reach adulthood. Secondary sex ratios were measured in 2010-2011 by collecting a growing feather (5^{th} or 6^{th} primary) from all possible chicks after the 14-day brooding period. Feathers were stored in 80% ethanol and frozen until DNA extraction. For sex determination, a universal PCR protocol was used to amplify homologs of the chromo-helicase-DNA-binding genes (CHD; Griffiths *et al.* 1998). PCRs were done in 10 µL volumes, each containing approximately 100 ng of genomic DNA, 200 µM of each dNTP (AB gene, supplied by Southern Cross Biotechnologies, Cape Town, South Africa), 5 pmoles of each primer, 1 U Taq DNA polymerase (Super-Therm JMR-801, Southern Cross Biotechnologies, Cape Town, South Africa), 1 × PCR reaction buffer, 1.5 mM MgCl2, and 0.1 µL BSA (10mg/ml). PCR cycling was done at initial denaturation of 95° C for 3 min, followed by 30 cycles at denaturation at 95° C for 15 s, annealing at 49° C for 30 s, elongation at 72° C for 15 s; and final extension at 72° C for 10 min. Amplified DNA fragments were run a 3% agarose gels at 100V for four hours and inspected under UV light. Female birds have one W and one Z chromosome, whereas male birds have two Z chromosomes. Because CHD copies on Z and W chromosomes differ in length, female birds show two distinct bands and male birds a single band following separation on agarose gels (Supplementary Figure A1).

A generalized linear model (GLM) with a binomial distribution and a logit link was used to examine potential sex ratio bias, the relationship between secondary sex ratio and extrinsic factors, and differences in male and female nestling survival, following Wilson and Hardy (2002). For secondary sex ratio analysis, partial broods (where one nestling died or disappeared before sampling) were included, following Fiala (1980). Explanatory variables were then sequentially excluded in order of decreasing significance until only terms with $p<0.1$ remained in the model. Excluded terms were then re-entered one by one in the final model to confirm that they did not explain a significant part of the variation. The full model included female body mass, study area, and habitat type (king or rockhopper penguin colony).

Survival

Apparent survival rates of sheathbills were estimated using capture–recapture Cormack-Jolly-Seber (CJS) open population models (Lebreton et al., 1992). Sheathbills were separated into three age classes (juveniles; 0-1 years of age, subadults; 2-3 years of age, and adults; ≥ 4 years of age). Survival was estimated at seasonal (winter; May to October, summer; November to April) intervals to account for the possibility that survival rates vary throughout the year. Transients are individuals that leave the study area after first capture and thus have a subsequent local survival probability equal to 0 (Pradel et al., 1997). Some sheathbill juveniles are highly transient post-fledge which has the potential to severely bias survival estimates (Choquet et al., 2009). The analysis of first year survival was therefore limited to birds that had been ringed prior to fledge. Directional tests (Z-tests) in the program U-CARE 2.2.5 (Choquet et al., 2005) showed no transient effects in juveniles, subadults or breeding adults.

Apparent survival of breeding and non-breeding sheathbills was analyzed separately after preliminary analysis found these birds to be influenced by different environmental parameters. Nonbreeding sheathbill survival was estimated using a three-age-class model. Model selection started from the model ϕ(age*t), p(habitat*t), where ϕ represents local survival rate, p represents the encounter rate, and t represents a six-month time interval. This was the most general model that supported the data. A goodness-of-fit test using the median $\hat{c}$ approach in program MARK 6.2 (White and Burnham, 1999) showed that the starting model fitted the data well and overdispersion was low (estimated $\hat{c}$ = 1.28). Breeding sheathbill survival was started with the CJS model ϕ(habitat*t), p(habitat*study site*t), which yielded a median $\hat{c}$ estimate of 1.37. The median $\hat{c}$ estimate was used for each respective model to correct the confidence intervals of my parameter estimates. All models were constrained to yield mean seasonal survival estimates. Model selection was based on Akaike's Information Criterion adjusted for overdispersion and sample size (QAICc, Burnham and Anderson, 2002). Model-averaged parameter estimates are presented to account for the model selection uncertainty (Burnham and Anderson, 2004). All models were run in program MARK 6.2 (White and Burnham, 1999).

Matrix population model

The Marion Island sheathbill population growth rate was estimated using a two-sex matrix projection model (Caswell, 2001). A two-sex model was chosen because a female-biased sex

ratio was observed in the adult population and the breeding rates of sheathbills may therefore vary with sex. It was assumed that male breeding is limited by the number of available breeding sites, whereas female breeding is limited by the availability of breeding males. The model assumed a pre-breeding census, an annual projection interval, and that all sheathbills breed at 4 years of age (Burger, 1979). The model is:

$$n_{t+1} = An_t$$

(equation 1)

where n is a vector with the number of individuals in each age-class in month t, and A is the projection matrix:

$$A = \begin{bmatrix} 0 & 0 & F_{fd} & 0 & 0 & \acute{\alpha}_m F_{md} \\ \phi_{f2w}\, x\, \phi_{fr2s} & 0 & 0 & 0 & 0 & 0 \\ 0 & \phi_{f3w}\, x\, \phi_{fr3s} & \phi_{f4w}\, x\, \phi_{fr4s} & 0 & 0 & 0 \\ 0 & 0 & F_{frb} & 0 & 0 & \acute{\alpha}_m F_{mb} \\ 0 & 0 & 0 & \phi_{m2w}\, x\, \phi_{m2s} & 0 & 0 \\ 0 & 0 & 0 & 0 & \phi_{m3w}\, x\, \phi_{m3s} & \phi_{m4w}\, x\, \phi_{m4s} \end{bmatrix}$$

(equation 2)

The matrix consists of 4 blocks of dimension 3x3. The upper left block describes the dynamics of the female segment of the population (subscript f), the lower right block describes the male segment (subscript m), the lower left is the females' contribution to sons, and the upper right is the males' contribution to daughters. In this study, $\acute{\alpha}_m$ is the probability of an individual male breeding. Two subadult stages (2-yr old subadult; subscript 2, 3-yr-old subadult; subscript 3) and one adult stage (subscript 4) were distinguished for each group. Transitioning from one age class to another depends on survival (ϕ) in winter (subscript w) and summer (subscript s). F describes the production of daughters (subscript d) and sons (subscript b) by females and males. To give an example of how these terms are calculated:

$$F_{\mathrm{fd}} = (n_{\mathrm{fd}}\, x\, \phi_{\mathrm{f1w}}\, x\, \phi_{\mathrm{f1s}})\, x\, min\left[\frac{n_{\mathrm{f4}}}{n_{\mathrm{f4}} + n_{\mathrm{m4}}}, \frac{n_{\mathrm{m4}}}{n_{\mathrm{f4}} + n_{\mathrm{m4}}}\right]$$

(equation 3)

where n_{fd} is the number of daughters produced by females, ϕ_{f1w} and ϕ_{f1s} are survival of juvenile (subscript 1) sheathbills in winter and summer, respectively. The last term is the

birth function which assumes that the rarer sex limits reproduction, where n_{f4} is the number of adult females and n_{m4} the number of adult males. The other fertility functions (F_{md}, F_{fb}, F_{mb}) were identical to equation (2) with ϕ and n replaced by the appropriate terms. This particular birth function was chosen because sheathbills require the full commitment of both parents in order to raise a successful brood.

The matrix model is non-linear. F depends on the population vector n, making it frequency-dependent but not density-dependent (Caswell and Weeks, 1986). Its dynamics thus depend on the sex ratio, but are independent of the absolute values of n. Simulations were preformed to estimate the population growth rate λ (Morris and Doak, 2002). Simulations started with a total population size of 1, and recorded the population growth rate after iteration 500, at which point a stable age and sex distribution had always been reached. The confidence interval for λ was calculated using parametric bootstrap methods. For each demographic parameter in the model, 10 000 random values were drawn from a normal distribution (on the logit scale) with mean and variance equal to the observed values. With these values, 10 000 matrices were reconstructed and log(λ) was calculated for each of them. After sorting these values by magnitude, the 250 and 9750 bootstrap replicates represent the lower and upper 95% confidence limit.

The matrix model used the model-averaged seasonal (six-month) survival rates for the three age classes (juvenile, subadult, adult) from the capture-mark-resighting models. A common survival rate was used for subadult age classes (2 and 3 yr-olds) because these stages were not distinguishable in the field and because the study was too short to have enough birds of precisely known age in the age class. The age structure of the sheathbill population was estimated as the mean proportion of adults and subadults ringed in the three study areas applied to the whole-island population estimate. Production of male and female fledglings in each of the two habitats was estimated as the mean number of fledglings produced per nest between the three study areas multiplied by the tertiary sex ratios observed in 2010-11. The probability of breeding for male sheathbills was estimated as the sum total of available breeding sites divided by the total number of adult males on the island. To estimate the number of available sheathbill breeding sites in rockhopper penguin colonies the total number of rockhopper breeding pairs (Crawford et al., 2009) was divided by the mean number of rockhopper penguins per sheathbill breeding site in the study areas. The number of available sheathbill breeding sites in king penguin colonies was estimated

from winter counts of breeding pairs, as suitable breeding sites are the limiting factor for sheathbill breeding in these areas (Burger, 1979). Because vital rates differed between RH and KP sheathbills, whole-island values were calculated using a weighted mean to account for the disparity between RH and KP sheathbill population sizes.

Metapopulation model

Preliminary analysis found the population growth rate to differ between habitat types, with negative and positive growth rates amongst RH and KP sheathbills, respectively, suggesting a source-sink dynamic (Pulliam, 1988). In order to explore this potential dynamic the matrix model described earlier was extended to allow movement of RH and KP sheathbills between the two habitats (Fig 2). It was assumed that movement occurred only between age classes 3 and 4, before the onset of maturity. The number of KP sheathbill breeding sites was assumed to be fixed and that any excess KP sheathbills moved into rockhopper penguin colonies and became RH sheathbills. Similarly, RH sheathbills could move into king penguin colonies if nest sites were available.

In addition, the number of rockhopper penguins on Marion Island has declined significantly over the past several decades (Cooper et al., 1997; Crawford et al., 2003, 2009). At the current estimated rate of decline, the number of birds on Marion Island may be halved within 15 years, and again in 30. It is unknown if there is a direct relationship between changes in penguin density and the number of breeding RH sheathbills. However, rockhopper penguin density undoubtedly has a considerable effect (Burger, 1979) and declines in penguins will eventually lead to declines in the number of sheathbill breeding sites. Therefore, in addition to the baseline model, sheathbill responses to scenarios of 50 % (n = 500) and 75 % (n = 250) reductions in available RH sheathbill breeding sites were projected.

All model projections were run for a 300-year time period and assumed that demographic rates did not change over time. All matrix analyses were performed in the statistical software R2.12.0. R code for the analyses is provided in Appendices D (population model) and E (metapopulation model).

Results

Foraging Behaviour

The total number of sheathbills in the east study area was significantly lower in 1994-95 and 2008-11 than in 1976-77 in both winter ($F_{(2,65)}$ = 35.53, Tukey's hsd, p = <0.001, n = 68) and summer ($F_{(2,64)}$ = 71.63, Tukey's hsd, p = <0.001, n = 67, Fig 3a). Winter use of vegetation was significantly lower in 1994-95 and 2008-11 than in 1976-77 ($F_{(2,65)}$ = 33.73, Tukey's hsd, p = <0.001, n = 68). There was a significant difference in summer use of vegetation between 1976-77 and 2008-11 ($F_{(2,64)}$ = 6.51, Tukey's hsd, p = 0.003, n = 67). The number of sheathbills using the intertidal zone did not differ between study periods. Winter use of rockhopper colonies was significantly higher in 1976-77 than in 1994-95 ($F_{(2,65)}$ = 12.77, Tukey's hsd, p = 0.002, n = 68), and 2008-11 (Tukey's hsd, p = <0.001). The number of sheathbills overwintering in king penguin colonies was significantly higher in 2008-11 than in 1976-77 ($F_{(2,65)}$ = 25.52, Tukey's hsd, p = <0.001, n = 68), and 1994-95 (Tukey's hsd, p = <0.001). There was no significant difference in the number of sheathbills in king penguins colonies in the summer season between 1976-77 and 2008-11, but 1994-95 was significantly lower than the other two study periods ($F_{(2,64)}$ = 3.68, Tukey's hsd, p = <0.001, n = 67).

Comparisons between 1976-77 and 2008-11 using a more comprehensive habitat classification revealed further significant changes in sheathbill foraging (Table 1). In the winter season, the number of sheathbills foraging in king penguin colonies increased by 75.7 % between study periods. Due to the overall decline in sheathbill numbers within the study area, this equated to a 279.5 % increase in the proportion of sheathbills utilizing the resource. Conversely, foraging for terrestrial invertebrates within all vegetative habitats declined significantly. The number and proportion of sheathbills in biotic vegetation declined 81.5 % and 83.0 %, respectively. The mire habitat suffered the greatest relative decline, with a 96.3 % reduction in both the number and proportion of sheathbills.

Changes in sheathbill summer foraging were also significant. The number of sheathbills foraging in king penguin colonies was unchanged, as was the number of birds utilizing the intertidal zone. However, because the total number of birds in the study area declined, the proportional use of these two habitats increased 32.8 % and 95.4 %, respectively. Conversely, the number and proportion of sheathbills foraging in rockhopper penguin colonies declined by 67.7 % and 67.0 % respectively. The number of birds foraging for terrestrial invertebrates during the summer season also declined, with 68.9 % and 50.0 % fewer birds in the biotic and mire habitats, respectively.

Foraging surveys in the North and West study areas and whole-island winter surveys in 2008-11 confirmed the low contemporary importance of terrestrial invertebrates to sheathbills (Supplementary Tables A4:A5). Whilst 21.8 % (± 16.6, *n* = 23) and 19.6 % (± 17.3) of sheathbills foraged in biotic and saltspray vegetation, respectively, in the West study area during the winter season, this high level of use was limited to Fur Seal Peninsula. This area undoubtedly benefits from the manuring of *c.* 40 000 sub-Antarctic fur seals. The mean island proportion of sheathbills in biotic and saltspray habitats in winter was 10.4 % (± 5.5, *n* = 4) and 6.9 % (± 2.5), respectively. In no study area did the proportion of sheathbills foraging in mire habitat exceed 3.0 % (± 4.6; West study area, *n* = 23), with an island mean of 1.1 % (± 0.9, *n* = 4).

Energetics

The mean monthly energy (kJ ha^{-1}) available in the form of macroinvertebrates between 1976-77 and 2006-07 declined by 96.6 % and 83.7 % in the mire and biotic habitats, respectively (Table 2). Over the same period, the monthly energy collectively consumed by invasive mice increased by 730.3 % in the mire habitat, but declined by 4.5 % in the biotic. The mean winter body mass of a RH sheathbill in 2008-11 was 447.5 g. The time-energy-budget analysis estimated a daily FMR of 571.2 kJ d^{-1} ind^{-1}, or 17 422 kJ $month^{-1}$, for RH sheathbills. Based on this estimate, and the mean monthly available energy available from macroinvertebrates (Table 2), one sheathbill would currently need to consume 53.2 % of the mean monthly standing crop over a 1 ha area to meet their energetic needs in the mire habitat. In the biotic habitat, one sheathbill would require 1.6 % of the monthly standing crop over the same area. However, mice were estimated to collectively remove a significant amount of invertebrate biomass from the mire (100 %) and biotic habitats (11.4 %), respectively (Table 2).

Body mass

The mean body mass of breeding RH females in early summer was significantly lower in 1994-95 and 2008-11 when compared to 1976-77 ($F_{(2,46)}$ = 4.32, Tukey's hsd, *p* = <0.02, *n* = 49; Table 3). A significant decline between 1976-77 and 2008-11 was also observed in the remaining three seasons (t_{27} = 2.28, *p* = 0.03, late summer; t_{23} = 2.14, *p* = 0.04, early winter; t_{19} = 4.25, *p* = 0.001, late winter). Female KP sheathbill body mass was also lower in 2008-11 than 1976-77 throughout the years, but only significantly so in early winter (t_{38} = 2.14, *p* =

0.05). By contrast, there was no significant difference in mean body mass between years for breeding male RH or KP sheathbills, with the exception of late summer season where mass declined significantly in both RH (t_{21} = 2.40, p = 0.03) and KP males (t_{39} = 2.23, p = 0.03).

Population size and structure

The absolute winter sheathbill population was approximately 4 000 individuals. Population estimates between years did not significantly differ (Table 4).

The adult sex ratio in 2008-11 was significantly biased in the eastern study area (72 males, 131 females, χ_1^2 = 17.15, p = <0.001) and the island as a whole (292 males, 393 females, χ_1^2 = 14.89, p = <0.001). In total, 134 chicks from 97 nests were genetically sexed in 2010-11 (Table 5). Both the secondary (42 males, 91 females, χ_1^2 = 18.05, p = <0.001) and tertiary (34 males, 85 females, χ_1^2 = 21.86, p = <0.001) sex ratios were significantly biased. Habitat and study area did not significantly influence primary sex ratio. However, there was a significant positive relationship between the production of males and female body mass (coefficient = 0.200 ± 0.006, χ_1^2 = 13.00, p = <0.001, n = 128). Post-brooding survival of male and female nestlings differed significantly amongst RH sheathbills (χ_1^2 = 47.08, p = 0.005, n = 92), but not KP sheathbills (Table 6).

Breeding and survival

Preliminary analyses found significant differences in several breeding parameters between sheathbills breeding in the two habitat types in 2008-11. This makes changes in breeding difficult to assess as previous studies did not consistently differentiate between habitat types. Nevertheless, referring only to the eastern study area, sheathbill clutch size was significantly smaller in 1994-95 and 2008-11 than in 1976-77 (Table 5). However, changes in egg mass and mean fledglings per nest, while lower, were not significant. Non-breeding sheathbill survival model selection favoured models that distinguished between age classes, habitat type, study area, and season (Table 7). In general, survival of immature age classes was higher among KP sheathbills than RH sheathbills (Table 8). Recapture probabilities varied between age classes, study area, habitat, and six-month recapture period and ranged from 0.313 (95 % CI = 0.227 – 0.415) to 0.971 (0.934 - 0.987) in non-breeders, and 0.539 (0.405 – 0.667) to 0.991 (0.969 – 0.998) in breeding adults.

Population growth rate and projections

Estimates of mean demographic rates for Marion Island sheathbills used in matrix population models are presented in Table 8. The population growth rate (λ) obtained by the matrix population model (equations 1 and 2) using the mean observed values for survival and reproduction indicated a 3.0 % per annum decline in the breeding population (λ = 0.970, bootstrap 95 % CI = 0.940 to 0.990).

The projection model predicted that at current vital rates the number of adult males on Marion Island, and therefore breeding pairs, will decline by 34.8 % by year 20, with a 60.8 % decline by the end of the projection (Fig 4). The number of adult females was predicted to initially increase, peaking at 10.1 % above starting values in year 26 before declining. Adult sex ratio was predicted to stabilize at 73.9 % female by year 88. The absolute number of sheathbills was predicted to decline, but by a rate three times slower than that of adult males over the first 25 years. Declines in the number of sheathbill breeding sites in rockhopper penguin colonies by 50 % and 75 % were predicted to decrease the number of potential breeding pairs by 13.0 % and 17.0 %, respectively, by the end of the projection.

Discussion

Sheathbill foraging ecology

In keeping with 1994-95 observations (Huyser et al., 2000), the current study confirmed that the importance of terrestrial invertebrates as a winter prey resource for sheathbills on Marion Island has significantly declined. Considering the vegetation habitats collectively, the number and proportion of sheathbills foraging for terrestrial invertebrates declined by 80.8 % and 79.7 %, respectively, between 1976-77 and 2008-11 (Table 1). Terrestrial invertebrates formerly supplied approximately 25 % of sheathbill annual energy needs (Burger, 1978) and upwards of 60 % of birds foraged in large flocks in the inland vegetation during the winter season (Burger, 1981a). In 2008-11 sheathbill use of these habitats was either greatly reduced (biotic) or largely incidental (mire, Table 1). Further, this behavioural shift was not exclusive to the eastern study area but rather a reflection of island-wide change. The underlying mechanism for such a shift is undoubtedly the loss of terrestrial invertebrate prey to invasive mice as first speculated by Huyser *et al.* (2000). Long-term data of invertebrate biomass confirms a significant decline in all major macro-invertebrate prey groups in all terrestrial habitats as a direct result of mouse predation (Chapter 2). Further, energetic modelling demonstrated that mice remove a significant proportion of the standing

crop in both the biotic and especially mire habitats, effectively displacing sheathbills. The dramatic decline in soil worms (potworms and earthworms; Enchytraeidae and *Microscolex kerguelarum*) specifically has likely had the largest impact on sheathbill foraging. Once contributing up to half of all invertebrates consumed by sheathbills by mass (Burger, 1978), soil worm annual biomass declined 88.0 % and 85.0 % in the biotic *Poa cookii* and *Cotula plumosa* vegetation respectively between 1976-77 and 2006-07 (Chapter 2). Moreover, in mire vegetation, annual biomass in *Jamesoniella colorata* declined 94.3 % and dropped below sampling detection in *Sanionia uncinatus* over the same period.

Mice have been present on Marion Island for almost 200 years. However, the scale of mouse impacts on the Marion Island ecosystem has greatly increased in the past few decades. It has recently been demonstrated that peak mouse densities on the island have greatly increased due to the local effects of global climate change (Chapter 2). As Marion Island has become warmer and drier, mice have increased the length of their breeding season by as much as three months in some habitats. Initiating the breeding season earlier increases the possibility of adding additional sexually mature cohorts to the population before the end of the breeding season, greatly increasing the peak population density. In addition, drying may increase the value of formally marginal habitat. As a result, ameliorating conditions brought on by climate change have lead to a 145.6 % increase in invasive mouse numbers over the past decade (Chapter 2). While evidence suggests minor shifts in their diet, mice continue to forage primarily on invertebrates of which they are the primary drivers of biomass. Thus, through a climate-driven population increase, invasive mice have displaced a native species from a foraging resource through exploitative competition.

The significant increase in the number of sheathbills overwintering in king penguin colonies is almost certainly in response to the loss of terrestrial invertebrates and not an increase in penguins, as that population has remained relatively stable over time (Crawford et al., 2009). Further, the shift from the terrestrial vegetation to king penguin colonies was not limited to the eastern study area but appears to be island-wide. For example, the mean number of sheathbills recorded during winter surveys at the largest king penguin colony (Kildalkey Bay) increased from 222.7 (± 70.8 SD) in 1994-1996, to 525.2 (± 63.0) in 2008-11. Currently, king penguin colonies are the most important wintering habitat on Marion Island, with 43.8 % of all birds (Fig. 3). Paradoxically, the total percentage of sheathbills in king

penguin colonies in 1976 was estimated as 48% (Burger, 1981a). However, this estimate was compiled from surveys that included days with snow cover and some counts may not have been accurate (A. Burger, personal communication). Such conditions may have forced sheathbills from the vegetation into penguin colonies, while also making it difficult to observe the white-plumaged birds in snow-covered areas.

Ad hoc surveys of the large king penguin colonies at Kildalkey and King Penguin bays suggest many wintering sheathbills leave these large colonies for rockhopper penguin colonies during the breeding season. Despite infrequent surveys that were restricted to the periphery of colonies, 9.7 % of all sheathbills ringed in the three study areas were resighted at least once in one of these two colonies. Of those birds, 73.8 % were adults and 39.2 % were confirmed breeders from one of the three study areas. Further, distance from colonies did not appear to inhibit visitation, with 38.5 % of resighted birds, and 50.0 % of resighted confirmed breeders, originating in the west study area on the opposite side of the island. Breeding adults on Marion Island previously remained within 1 km of breeding territories throughout the year (Burger, 1979), as do sheathbills on other islands (Jouventin et al., 1996), suggesting these cross-island seasonal movements are a novel response to low winter food availability.

The shift in focus towards king penguins had a significant cost to sheathbill winter resources, at least in all but the two largest king penguin colonies. Whereas the mean number of penguins per sheathbill was estimated to be 48.0 in 1974-77 (Burger, 1984), the 2008-11 estimate was 29.0, a 39.6 % decline in potential foraging resources.

The decline in sheathbills foraging in rockhopper penguin colonies during the breeding season was significant and parallel with population declines in that species. The number of rockhopper penguin breeding pairs on Marion Island decreased by between 63 % and 74 % from 1994-95 to 2008-09 (Crawford et al., 2009), reflecting a recent global decline (Cunningham and Moors, 1994; Pütz et al., 2003; Cuthbert et al., 2009; Dehnhard et al., 2013). The mechanisms for such a wide-scale reduction in penguin populations are unclear, but have been linked to changes in primary productivity and krill stocks (Cunningham and Moors, 1994; Hilton et al., 2006; Cresswell et al., 2008), which in turn are changing in response to changes in climate and sea ice conditions (Fraser and Hofmann, 2003; Atkinson et al., 2004; Siegel, 2005). Increased predation pressure from a growing fur seal population

has also been suggested for some islands (Cuthbert et al., 2009). Despite significantly fewer sheathbills foraging in rockhopper colonies, the number of penguins per sheathbill was reduced from an estimated 180.0 in 1974-77 (Burger, 1981b) to 74.0 in 2008-11, a decline of 58.9 %. Further, because sheathbills benefit from the increased kleptoparasitism opportunities and excreta associated with more penguin nestlings persisting to fledge, the associated long-term decline in penguin breeding success (Crawford et al., 2008) undoubtedly compounds the loss in penguin numbers.

Condition, breeding, and sex ratios

Body mass has been shown to be a reliable index of body condition in birds (Schamber et al., 2009; Labocha and Hayes, 2011). The general decline in sheathbill body condition, as indicated by changes in mass, corresponded with the decline in overall food abundance, but the effects were not uniform. Female RH sheathbills were in significantly poorer condition in 2008-11 than in 1976-77 throughout the year, with the decline most significant in late winter. RH sheathbills previously maintained or even gained in mass whilst foraging on terrestrial invertebrates (Table 3) suggesting that the loss of this resource becomes more costly as the winter progresses. The parallel decline in female KP sheathbill body condition was most likely also the result of the decline in terrestrial invertebrates, but in another form. As sheathbills that formally foraged on terrestrial invertebrates moved to overwinter in king penguin colonies, the number of penguins available per sheathbill also declined. That males failed to decline in body condition in most seasons is possibly due to being larger and more aggressive than females (Burger, 1980). Larger males outcompeting females for scarce resources is not uncommon in birds (Benkman, 1997; Marra and Holmes, 2001; Donald et al., 2007). Within sheathbills, though breeding pairs cooperate to defend their territories, males are dominant within the pair and feed first. Indeed, male KP sheathbills were observed on several occasions chasing their mate from newly available food, including during the egg formation period when a pair's reproductive success largely depends on a female's access to food (Martin, 1987). The same size advantage may give RH sheathbill males more foraging options during the winter season as they were more likely to be resighted in king penguin colonies than females. For example, 69.4 % of western study site birds resighted in king penguin colonies were adult males. Resight surveys suggest such visitations may have lasted only one or two weeks and were possibly "maintenance trips". Thus, changes in body condition demonstrate how the consequences of declining food

abundance are disproportionate amongst sheathbills, with the smaller females bearing the brunt of change.

Despite a significant impoverishment of foraging resources and a decline in female body condition, the reproductive output of Marion Island sheathbills did not significantly decrease between study periods. Life history theory predicts that the reproductive decisions of an individual should be adapted to both intrinsic (e.g., body condition, number of offspring) and extrinsic (e.g., weather conditions, habitat quality) properties (Stearns, 1992). When faced with suboptimal environmental conditions, long-lived species such as sheathbills are predicted to modify their breeding effort rather than jeopardize their future reproductive value (Drent and Daan, 1980). Decreasing clutch size and adjusting sex ratios, as observed in this study, are two potential methods to minimize resource expenditure without sacrificeing offspring number and quality. Clutch-size reduction is a common response to food limitation in birds (Lack, 1947; Klomp, 1970; Högstedt, 1980), and numerous hypotheses have been suggested to explain the phenomenon, though all variants of the concept that clutch size reduction maximizes fitness (Winkler, 1985). Reducing the number of eggs produced may allow individuals to maintain chick production and fitness under poor environmental conditions by allowing for increases in other forms of effort such as egg quality, resources per nestling, or allowing females to conserve greater energy reserves which may translate into greater parental care (Lack, 1947; Cody, 1966; Winkler and Walters, 1983; Martin, 1987). Similarly, the total effort of raising a brood is determined not only by brood size, but the sex ratio of that brood (Øigarden and Lifjeld, 2012). If sexes differ in nutritional requirements, either at the egg or nestling stage, sex ratio adjustment towards the less costly sex can greatly reduce parental effort and juvenile mortality (Nager et al., 2000; Kalmbach et al., 2001; Badyaev et al., 2002).

Though a bias towards the production of daughters was clear in this study, it was not possible to confirm at what stage of development such bias may have occurred. In birds, females are the heterogametic sex and sex-ratio adjustment is presumably under maternal control (Oddie, 1998). Although the proximate mechanism involved in sex-ratio manipulation in vertebrates with chromosomal sex determination remains unclear (Alonso-Alvarez, 2006), and constraints on adjustment clearly exist (West and Sheldon, 2002), there is strong empirical evidence that birds can manipulate the sex of their offspring at the primary sex-ratio stage (West et al., 2002; Pike and Petrie, 2003; Cassey et al., 2006).

Alternatively, the bias may occur at the secondary sex-ratio stage. Under this scenario, the bias favouring daughters would have occurred through elimination of males from an unbiased brood. Most sheathbills hatched two nestling, and one nestling died and disappeared in 30.5 % of nests before a sample could be collected and sex determined. It is possible a significant percentage of these nestling were male and suffered a disproportional mortality rate due to greater nutrient requirements associated with sexual dimorphism (Nager et al., 2000), greater sensitivity to adverse conditions (Fletcher and Hamer, 2004), or biased provisioning effort by parents in relation to offspring sex (Mainwaring et al., 2011). A bias at the primary sex-ratio stage may be more likely in food-limited sheathbills as the additional resources provisioned to a male embryo would not be wasted. However, male sheathbill nestling survival was significantly lower, at least within RH sheathbills, suggesting a bias at the secondary stage.

While such reproductive trade-offs may be beneficial to individuals within a given year, under chronic environmental degradation the repeated practice of producing significantly more daughters will ultimately affect population structure and numbers. This may be especially true for monogamous species such as sheathbills where males are as valuable as females for reproduction (Rankin and Kokko, 2007). The adult sex ratio was found to be significantly biased in the Marion Island sheathbill population in 2008-11, both in the eastern study area, and the island as a whole. By contrast, a random sample of adult sheathbills taken on mouse-free Prince Edward Island in 2010 was unbiased (32 males, 21 females, χ_1^2 = 1.92, p = 0.17; McClelland and Chown unpublished data), as was the population in the Kerguelen archipelago (Jouventin et al., 1996), suggesting that the current skew on Marion Island is a response to ecological change. Further, ringing data from 1974-77 suggests this skew is recent, as the adult sex ratio in the eastern study area was previously unbiased (111 males, 110 females, χ_1^2 = 0.57, p = 0.45; Alan Burger, unpublished data). Though both studies targeted breeding pairs in the summer season, attempts to ring all birds over the course of the two studies were made and the two datasets are presumed to be reliable estimations of sex ratios. As adult survival was found to be independent of sex, and in the absence of immigration and emigration, the most plausible driver of this change is the heavily biased sex ratio in offspring.

Population growth

There was no evidence of a decline in the absolute sheathbill population between the 1970s and the current study. In this regard, the previously speculated decline between 1976-77 and the mid-1990s (Huyser et al., 2000) is also uncertain. However, the reliability of population estimates from previous studies is limited by the lack of confidence intervals associated with counts. Multiple independent surveys in this study confirmed high variation in annual population surveys, with estimates differing as much as 17.8 % within years. This high variation suggests that the detection probability of sheathbills is highly dynamic. This is likely because many sheathbills often shelter in or forage amongst the numerous cracks and crevices provided by Marion Island's rocky coast and detection probabilities will vary with weather conditions, observer, or local habitats. Such variation can hide population trends (Link and Nichols, 1994; Shenk et al., 1998; Thompson et al., 1998). If this is the case for sheathbills, the demographic estimate of negative population growth determined by this study may have applied for some time.

Whilst decades-long losses in sheathbill numbers were not detected, population modelling suggests that sheathbills are currently declining. Further, the decline in the reproductive population is outpacing that of the absolute population. While the number of breeding pairs is projected to decline by an average of 2.6 % over the first decade, the decline in the absolute population is forecast to average 0.8 %. The ability of population surveys to detect such a subtle decline is questionable given the high variance associated with current counts.

The purpose of the demographic modelling was not to estimate the extinction probability of sheathbills *per se*, but to estimate the response of the sheathbill population to recent ecological change and the likely scenario of continued rockhopper penguin declines. The two-sex density dependant population model used here demonstrated the importance of accounting for source-sink dynamics and density-dependence, as well as the potential effects of sex ratio, in regulating populations. The model showed that because adult males outnumber the estimated number of breeding sites, density dependence is the greatest influence on the Marion Island sheathbill population under current conditions. However, because the production of offspring is highly biased towards females, the number of males is projected to eventually drop below this threshold, at which time the reproductive population will be limited by the relative availability of partners (Clutton-Brock and Parker, 1992). Termed the "marriage squeeze" (Schoen, 1983), the reproductive output of the

population will decrease, which will lead to further population declines (Hamilton, 1967; West, 2009).

The model also showed that production from KP sheathbills is sufficient to prevent the whole-island reproductive population from declining beyond 585 pairs. Indeed, because of this source dynamic from king penguin colonies, and in addition to exceptional adult survival, Marion Island sheathbills appear highly resistant to population crashes. Even under the scenario of breeding site losses of 75 % in rockhopper penguin colonies, the number of sheathbill breeding pairs is not projected to drop below more than 485. However, any decline in such a small population increases its risk of extinction (Pimm et al., 1988; Purvis et al., 2000; Traill et al., 2010). Though projection models predict the Marion Island sheathbill population to eventually stabilize, any further declines increase the population's susceptibility to demographic (Melbourne and Hastings, 2008), environmental (Lande, 1993), and genetic stochasticity (Spielman et al., 2004).

Conclusions

Results of this study suggest that Marion Island sheathbills are declining is response to the combined effects of invasive species and global climate change. However, several processes and parameters require further investigation to reduce uncertainty and improve our understanding of the long-term effects of ecosystem change for Marion Island sheathbills. For example, the survival and reproduction estimates were taken over a relatively short time frame and thus cannot account for ecological and demographic stochasticity. Further, the variance associated with estimates of penguin numbers on the island, vital to estimating the number of sheathbill nesting sites in the case of rockhopper penguins, is unknown. It must also be reiterated that population models assume that sheathbill vital rates do not change in response to changes in population size or possible environmental conditions, an unlikely prospect.

Further changes to the Marion Island environment and sheathbill ecology not addressed in this study are also possible. For example, global climate change is also predicted to have a negative impact on king penguin populations (Le Bohec et al., 2008). Such declines are unlikely to affect the number of sheathbills breeding in king penguin colonies on Marion Island, as the number of penguins far outweighs the number of sheathbill breeding sites. However, a decline in penguin numbers may have significant

consequences for sheathbills in the form of increased resource competition and declines in body condition. Modifications in sheathbill social behaviour are also possible. When one sex becomes the limiting resource for the other, increased competition amongst the more common sex, or mate choosiness amongst the limited sex, is possible (Kvarnemo and Ahnesjo, 1996). Further, the intensity of this intrasexual selection is expected to increase as the sex ratio deviates from equality (Emlen and Oring, 1977). However, ultimately how individuals respond to a long-term skew in sex ratios, and the demographic consequences of that response, remain poorly understood (Clutton-Brock et al., 2002; Cockburn et al., 2002; Le Galliard et al., 2005), leaving the long-term repercussions for Marion Island sheathbills difficult to predict.

Finally, there is a significant lack of ecological knowledge for many island species. For example, despite being a high conservation priority, island birds remain significantly less studied than their continental counterparts (Brooks et al., 2008; de Lima et al., 2011). This study makes clear the need to document island species ecology in order to understand their current and possibly future responses to global change. Many of the responses of sheathbills observed in this study are significant but subtle and would not have been evident through population monitoring alone, nor without the invaluable contribution of baseline historical data from previous work.

References

Alcover, J.A., Sans, A., Palmer, M., 1998. The extent of extinctions of mammals on islands. Journal of Biogeography 25, 913–918.

Alonso-Alvarez, C., 2006. Manipulation of primary sex-ratio: an updated review. Avian and Poultry Biology Reviews 17, 1–20.

Atkinson, A., Siegel, V., Pakhomov, E., Rothery, P., 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. Nature 432, 100–103.

Atkinson, I.A.E., 1985. The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifaunas, in: Moors, P.J. (Ed.), Conservation of Island Birds. Cambridge: International Council for Bird Preservation Technical Publication No. 3, pp. 35–81.

Badyaev, A. V, Hill, G.E., Beck, M.L., Dervan, A.A., Duckworth, R.A., McGraw, K.J., Nolan, P.M., Whittingham, L.A., 2002. Sex-biased hatching order and adaptive population divergence in a passerine bird. Science 295, 316–318.

Benkman, C.W., 1997. Feeding behavior, flock size dynamics, and variation in sexual selection in crossbills. Auk 114, 163–178.

Bergstrom, D.M., Lucieer, A., Kiefer, K., Wasley, J., Belbin, L., Pedersen, T.K., Chown, S.L., 2009. Indirect effects of invasive species removal devastate World Heritage Island. Journal of Applied Ecology 46, 73–81.

Bessa-Gomes, C., Legendre, S., Clobert, J., 2004. Allee effects, mating systems and the extinction risk in populations with two sexes. Ecology Letters 7, 802–812.

Blackburn, T.M., Cassey, P., Duncan, R.P., Evans, K.L., Gaston, K.J., 2004. Avian extinction and mammalian introductions on oceanic islands. Science 305, 1955–1958.

Blackburn, T.M., Gaston, K.J., 2005. Biological invasions and the loss of birds on islands: insights into the idiosyncrasies of extinction, in: Exotic Species: a Source of Insight into Ecology, Evolution, and Biogeography. Academic Press, London, pp. 85–110.

Le Bohec, C., Durant, M., Gauthier-Clerc, M., Stenseth, N.C., Park, Y., Pradel, R., Gremillet, D., Gendner, J.-P., Le Maho, Y., 2008. King penguin population threatened by Southern Ocean warming. Proceedings of the National Academy of Sciences of the United States of America 105, 2493–2497.

Brodier, S., Pisanu, B., Villers, A., Pettex, E., Lioret, M., Chapuis, J.-L., Bretagnolle, V., 2011. Responses of seabirds to the rabbit eradication on Ile Verte, sub-Antarctic Kerguelen Archipelago. Animal Conservation 14, 459–465.

Brook, B.W., Sodhi, N.S., Bradshaw, C.J.A., 2008. Synergies among extinction drivers under global change. Trends in Ecology and Evolution 23, 453–460.

Brooks, T.M., Collar, N.J., Green, R.E., Marsden, S.J., Pain, D.J., 2008. The science of bird conservation. Bird Conservation International 18, S2–S12.

Burger, A.E., 1978. Terrestrial invertebrates: a food resource for birds at Marion Island. South African Journal of Antarctic Research 8, 87–99.

Burger, A.E., 1979. Breeding biology, moult, and survival of lesser sheathbills *Chionis minor* at Marion Island. Ardea 67, 1–14.

Burger, A.E., 1980. Sexual size dimorphism and aging characteristics in the lesser sheathbill at Marion Island. Ostrich 51, 39–43.

Burger, A.E., 1981a. Food and foraging behaviour of lesser sheathbills at Marion Island. Ardea 69, 167–180.

Burger, A.E., 1981b. Time budgets, energy needs, and kleptoparasitism in breeding lesser sheathbills (*Chionis minor*). Condor 83, 106–112.

Burger, A.E., 1982. Foraging behaviour of lesser sheathbills *Chionis minor* exploiting invertebrates on a Sub-Antarctic island. Oecologia 52, 236–245.

Burger, A.E., 1984. Winter territoriality in lesser sheathbills on breeding grounds at Marion Island. Wilson Journal of Ornithology 96, 20–33.

Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: a practical information-theoretic approach., 2nd ed. Springer, New York.

Burnham, K.P., Anderson, D.R., 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociological Methods and Research 33, 261–304.

Cahill, A.E., Aiello-Lammens, M.E., Fisher-Reid, M.C., Hua, X., Karanewsky, C.J., Yeong Ryu, H., Sbeglia, G.C., Spagnolo, F., Waldron, J.B., Warsi, O., Wiens, J.J., 2013. How does climate change cause extinction? Proceedings of the Royal Society B 280, doi: 10.1098/rspb.2012.1890.

Cannon, R.J.C., 1998. The implications of predicted climate change for insect pests in the UK, with emphasis on non-indigenous species. Global Change Biology 4, 785–796.

Carlquist, S., 1974. Island biology. Columbia University Press, New York.

Carrete, M., Serrano, D., Illera, J.C., López, G., Vögeli, M., Delgado, A., Tella, J.L., 2009. Goats, birds, and emergent diseases: apparent and hidden effects of exotic species in an island environment. Ecological Applications 19, 840–853.

Case, T.J., 1996. Global patterns in the establishment and distribution of exotic birds. Biological Conservation 78, 69–96.

Cassey, P., Ewen, J.G., Møller, A.P., 2006. Revised evidence for facultative sex ratio adjustment in birds: a correction. Proceedings of the Royal Society B 273, 3129–3130.

Caswell, H., 2001. Matrix population models, 2nd ed. Sinauer, Sunderland.

Caswell, H., Weeks, D.E., 1986. Two-sex models: chaos, extinction, and other dynamic consequences of sex. American Naturalist 128, 707–735.

Choquet, R., Lebreton, J.-D., Gimenez, O., Reboulet, A.-M., Pradel, R., 2009. U-CARE: Utilities for performing goodness of fit tests and manipulating CApture-REcapture data. Ecography 32, 1071–1074.

Choquet, R., Reboulet, A., Lebreton, J.D., Gimenez, O., Pradel, R., 2005. U-CARE 2.2 User's Manual. CEFE, UMR 5175, CNRS, Montpellier, France.

Chown, S.L., Froneman, P.W., 2008. The Prince Edward Islands: land-sea interactions in a changing ecosystem. Sun Press, Stellenbosch.

Chown, S.L., Smith, V.R., 1993. Climate change and the short-term impact of feral house mice at the sub-Antarctic Prince Edward Islands. Oecologia 96, 508–516.

Clark, M.R., Dingwal, P.R., 1985. Conservation of islands in the Southern Ocean: a review of the protected areas of Insulantarctica. World Conservation Union, Gland, Switzerland.

Clavero, M., Brotons, L., Pons, P., Sol, D., 2009. Prominent role of invasive species in avian biodiversity loss. Biological Conservation 142, 2043–2049.

Clout, M.N., Veitch, C.R., 2002. Turning the tide of biological invasion: the potential for eradicating invasive species, in: Veitch, C.R., Clout, M.N. (Eds.), Turning the Tide: The Eradication of Invasive Species. IUCN Invasive Species Specialist Group, Gland, Switzerland and Cambridge, UK, pp. 1–3.

Clutton-Brock, T.H., Coulson, T.N., Milner-Gulland, E.J., Thomson, D., Armstrong, H.M., 2002. Sex differences in emigration and mortality affect optimal management of deer populations. Nature 415, 633–637.

Clutton-Brock, T.H., Parker, G.A., 1992. Potential reprodcutive rates and the operation of sexual selection. Quarterly Review of Biology 67, 437–456.

Coblentz, B.E., 1978. The effects of feral goats (*Capra hircus*) on island ecosystems. Biological Conservation 13, 279–286.

Cockburn, A., Legge, S., Double, M.C., 2002. Sex ratio in birds and mammals: can the hypotheses be disentagled?, in: Hardy, I.C.W. (Ed.), Sex Ratios: Concepts and Research Methods. Cambridge University Press, Cambidge, pp. 266–286.

Cody, M.L., 1966. A general theory of clutch size. Evolution 20, 174–184.

Cooper, J., Brown, C.R., 1990. Ornithological research at the sub-Antarctic Prince Edward Islands: a review of achievements. South African Journal of Antarctic Research 20, 40–57.

Cooper, J., Wolfaardt, A.C., Crawford, R.J.M., 1997. Trends in population size and breeding success at colonies of macaroni and rockhopper penguins, Marion Island, 1979/80 - 1995/96. CCAMLR Science 4, 89–103.

Courchamp, F., Chapuis, J., Pascal, M., 2003. Mammal invaders on islands: impact, control and control impact. Biological Reviews 78, 347–383.

Crafford, J.E., Scholtz, C.H., 1987. Quantitative differences between the insect faunas of Sub-Antarctic Marion and Prince Edward Islands: a result of human intervention? Biological Conservation 40, 255–262.

Crawford, R., Makhado, A., Upfold, L., Dyer, B., 2008. Mass on arrival of rockhopper penguins at Marion Island correlated with breeding success. African Journal of Marine Science 30, 185–188.

Crawford, R.J.M., Cooper, J., 2003. Conserving surface-nesting seabirds at the Prince Edward Islands: the role of research, monitoring, and legislation. African Journal of Marine Science 25, 415–426.

Crawford, R.J.M., Cooper, J., Dyer, B.M., Greyling, M.D., Klages, N.T.W., Nel, D.C., Nel, J.L., Petersen, S.L., Wolfaardt, A.C., 2003. Decreases in the number of eastern rockhopper

penguin *Eudyptes chrysocome filholi* at Marion Island, 1994/95-2002/03. African Journal of Marine Science 25, 487–498.

Crawford, R.J.M., Tree, A.J., Whittington, P.A., Visagie, J., Upfold, L., Roxburg, K.J., Martin, A.P., Dyer, B.M., 2008. Recent distributional changes of seabirds in South Africa: is climate having an impact? African Journal of Marine Science 30, 189–193.

Crawford, R.J.M., Whittington, P.A., Upfold, L., Ryan, P.G., Petersen, S.L., Dyer, B.M., Cooper, J., 2009. Recent trends in numbers of four species of penguins at the Prince Edward Islands. African Journal of Marine Science 31, 419–426.

Cresswell, K.A., Wiedenmann, J., Mangel, M., 2008. Can macaroni penguins keep up with climate- and fishing-induced changes in krill? Polar Biology 31, 641–649.

Cronk, Q.C.B., 1997. Islands: stability, diversity, conservation. Biodiversity and Conservation 6, 477–493.

Cunningham, D.M., Moors, P.J., 1994. The decline of rockhopper penguins *Eudyptes chrysocome* at Campbell Island, Southern Ocean and the influence of rising sea temperatures. Emu 94, 27–36.

Cuthbert, R., Cooper, J., Burle, M.-H., Glass, C.J., Glass, J.P., Glass, S., Glass, T., Hilton, G.M., Sommer, E.S., Wanless, R.M., Ryan, P.G., 2009. Population trends and conservation status of the northern rockhopper penguin *Eudyptes moseleyi* at Tristan da Cunha and Gough Island. Bird Conservation International 19, 109.

Darling, E.S., Côté, I.M., 2008. Quantifying the evidence for ecological synergies. Ecology Letters 11, 1278–1286.

Dehnhard, N., Poisbleau, M., Demongin, L., Ludynia, K., Lecoq, M., Masello, J.F., Quillfeldt, P., 2013. Survival of rockhopper penguins in times of global climate change. Aquatic Conservation: Marine and Freshwater Ecosystems DOI: 10.1002/aqc.2331.

Delgado García, J.D., 2002. Interaction between introduced rats and a frugivore bird-plant system in a relict island forest. Journal of Natural History 36, 1247–1258.

Diamond, J.M., 1989. The present, past and future of human-caused extinctions. Philisophical Transactions of the Royal Society B 325, 469–477.

Didham, R.K., Ewers, R.M., Gemmell, N.J., 2005. Comment on “Avian extinction and mammalian introductions on oceanic islands”. Science 307, 1412a.

Donald, P.F., 2007. Adult sex ratios in wild bird populations. Ibis 149, 671–692.

Donald, P.F., Hille, S., Taylor, R., Wells, C.E., Bolton, M., Marlow, T., 2007. Sexual dimorphism, niche partitioning and social dominance in the feeding ecology of the critically endangered Raso lark *Alauda razae*. Ibis 149, 848–852.

Donlan, C.J., Tershy, B.R., Croll, D.A., 2002. Islands and introduced herbivores: conservation action as ecosystem experimentation. Journal of Applied Ecology 39, 235–246.

Drent, R.H., Daan, S., 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68, 225–252.

Dukes, J.S., Mooney, H.A., 1999. Does global change increase the success of biological invaders? Trends in Ecology and Evolution 14, 135–139.

Duncan, R.P., Blackburn, T.M., 2004. Extinction and endemism in the New Zealand avifauna. Global Ecology and Biogeography 13, 509–517.

Duncan, R.P., Blackburn, T.M., 2007. Causes of extinction in island birds. Animal Conservation 10, 149–150.

Efford, M.G., Dawson, D.K., Robbins, C.S., 2004. DENSITY: software for analysing capture – recapture data from passive detector arrays. Animal Biodiversity and Conservation 1, 217–228.

Elton, C.S., 1958. The ecology of invasions by animals and plants. University of Chicago Press, Chicago.

Emlen, S.T., Oring, L.W., 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197, 215–223.

Fiala, K.L., 1980. On estimating the primary sex ratio from incomplete data. American Naturalist 115, 442–444.

Fletcher, K.L., Hamer, K.C., 2004. Offspring sex ratio in the common tern *Sterna hirundo*, a species with negligible sexual size dimorphism. Ibis 146, 454–460.

Fordham, D.A., Brook, B.W., 2008. Why tropical island endemics are acutely susceptible to global change. Biodiversity and Conservation 19, 329–342.

Fort, J., Porter, W.P., Grémillet, D., 2011. Energetic modelling: a comparison of the different approaches used in seabirds. Comparative Biochemistry and Physiology A 158, 358–365.

Frankham, R., 1995. Conservation genetics. Annual Review of Genetics 29, 305–327.

Fraser, W., Hofmann, E., 2003. A predator's perspective on causal links between climate change, physical forcing and ecosystem response. Marine Ecology Progress Series 265, 1–15.

Le Galliard, J.-F., Fitze, P.S., Ferrière, R., Clobert, J., 2005. Sex ratio bias, male aggression, and population collapse in lizards. Proceedings of the National Academy of Sciences of the U.S.A. 102, 18231–18236.

Gienapp, P., Teplitsky, C., Alho, J.S., Mills, J.A., Merilä, J., 2008. Climate change and evolution: disentangling environmental and genetic responses. Molecular Ecology 17, 167–178.

Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W., Holt, R.D., 2010. A framework for community interactions under climate change. Trends in Ecology and Evolution 25, 325–331.

Gleeson, J.P., van Rensburg, P.J.J., 1982. Feeding ecology of the house mouse *Mus musculus*, on Marion Island. South African Journal of Antarctic Research 12, 34–39.

Grant, P.R., 1998. Evolution on islands. Oxford University Press, Oxford.

Griffiths, R., Double, M.C., Orr, K., Dawson, R.J.G., 1998. A DNA test to sex most birds. Molecular Biology 7, 1071–1075.

Hamilton, W.D., 1967. A sex-ratio theory for sex linkage and inbreeding. Science 156, 477–488.

Hansen, D.M., Olesen, J.M., Jones, C.G., 2002. Trees , birds and bees in Mauritius: exploitative competition between introduced honey bees and endemic nectarivorous birds? Journal of Biogeography 29, 721–734.

Hansen, J., Sato, M., Ruedy, R., Lo, K., Lea, D.W., Medina-Elizade, M., 2006. Global temperature change. Proceedings of the National Academy of Sciences of the U.S.A. 103, 14288–14293.

Harmon, J.P., Moran, N.A., Ives, A.R., 2009. Species response to environmental change: impacts of food web interactions and evolution. Science 323, 1347–1350.

Harris, D.B., Macdonald, D.W., 2007. Interference competition between introduced black rats and endemic Galapagos rice rats. Ecology 88, 2330–2344.

Hellmann, J.J., Byers, J.E., Bierwagen, B.G., Dukes, J.S., 2008. Five potential consequences of climate change for invasive species. Conservation Biology 22, 534–543.

Hilton, G.M., Thompson, D.R., Sagar, P.M., Cuthbert, R.J., Cherel, Y., Bury, S.J., 2006. A stable isotopic investigation into the causes of decline in a sub-Antarctic predator, the rockhopper penguin *Eudyptes chrysocome*. Global Change Biology 12, 611–625.

Hofmeyr, G.J.G., Bester, M.N., Makhado, A.B., Pistorius, P.A., 2006. Population changes in Subantarctic and Antarctic fur seals at Marion Island. South African Journal of Wildlife Research 36, 55–68.

Högstedt, G., 1980. Evolution of clutch size in birds: adaptive variation in relation to territory quality. Science 210, 1148–1150.

Holdaway, R.N., 1999. Introduced predators and avifaunal extinction in New Zealand, in: McPhee, R.D. (Ed.), Extinctions in Near Time. Kluwer Academic/Plenum, New York, pp. 189–238.

Holt, R.D., 1996. Food webs in space: an island biogeographic perspective, in: Polis, G.A., Winemiller, K.O. (Eds.), Food Webs: Integration of Pattern and Process. Chapman & Hall, London, pp. 313–323.

Honegger, R.E., 1981. List of amphibians and reptiles either known or thought to have become extinct since 1600. Biological Conservation 19, 141–158.

Huyser, O., Ryan, P.G., Cooper, J., 2000. Changes in population size, habitat use and breeding biology of lesser sheathbills (*Chionis minor*) at Marion Island: impacts of cats, mice and climate change? Biological Conservation 92, 299–310.

Johnson, M.S., Thomson, S.C., Speakman, J.R., 2001. Limits to sustained energy intake. Journal of Experimental Biology 204, 1925–1935.

Jones, H.P., Tershy, B.R., Zavaleta, E.S., Croll, D.A., Keitt, B.S., Finkelstein, M.E., Howald, G.R., 2008. Severity of the effects of invasive rats on seabirds: a global review. Conservation Biology 22, 16–26.

Jouventin, P., Bried, J., Ausilio, E., 1996. Life-history variations of the lesser sheathbill *Chionis minor* in contrasting habitats. Ibis 138, 732–741.

Kalmbach, E., Nager, R.G., Griffiths, R., Furness, R.W., 2001. Increased reproductive effort results in male-biased offspring sex ratio: an experimental study in a species with reversed sexual size dimorphism. Proceedings of the Royal Society B 268, 2175–2179.

Kier, G., Kreft, H., Lee, T.M., Jetz, W., Ibisch, P.L., Nowicki, C., Mutke, J., Barthlott, W., 2009. A global assessment of endemism and species richness across island and mainland regions. Proceedings of the National Academy of Sciences of the U.S.A. 106, 9322–9327.

King, W.B., 1985. Island birds: will the future repeat the past?, in: Conservation of Island Birds. ICBP Technical Publication No. 3, pp. 3–15.

Klomp, H., 1970. The determination of clutch size in birds. Ardea 58, 1–124.

Komdeur, J., Daan, S., Tinbergen, J., Mateman, C., 1997. Extreme adaptive modification in sex ratio of the Seychelles warbler's eggs. Nature 385, 522–525.

Kreft, H., Jetz, W., Mutke, J., Kier, G., Barthlott, W., 2008. Global diversity of island floras from a macroecological perspective. Ecology Letters 11, 116–127.

Kurle, C.M., Croll, D.A., Tershy, B.R., 2008. Introduced rats indirectly change marine rocky intertidal communities from algae- to invertebrate-dominated. Proceedings of the National Academy of Sciences of the U.S.A. 105, 3800–3804.

Kvarnemo, C., Ahnesjo, I., 1996. The dynamics of operational sex ratios and competition for mates. Trends in Ecology and Evolution 11, 404–408.

Labocha, M.K., Hayes, J.P., 2011. Morphometric indices of body condition in birds: a review. Journal of Ornithology 153, 1–22.

Lack, D., 1947. The significance of clutch size. Ibis 89, 309–352.

Lammers, T.G., Freeman, C.E., 1986. Ornithophily among the Hawaiian Lobelioideae (Campanulaceae): evidence from floral nectar sugar compositions. American Journal of Botany 73, 1613–1619.

Lande, R., 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist 142, 911–927.

Lebreton, J., Burnham, K.P., Clobert, J., Anderson, D.R., 1992. Modeling survival and testing biological hypotheses using marked animals - a unified approach with case studies. Ecological Monographs 62, 67–118.

De Lima, R.F., Bird, J.P., Barlow, J., 2011. Research effort allocation and the conservation of restricted-range island bird species. Biological Conservation 144, 627–632.

Link, W.A., Nichols, J.D., 1994. On the importance of sampling variance to investigations of temporal variation in animal population size. Oikos 69, 539–544.

Loehle, C., Eschenbach, W., 2012. Historical bird and terrestrial mammal extinction rates and causes. Diversity and Distributions 18, 84–91.

MacArthur, R.H.W., Wilson, E.O., 1967. The theory of island biogeography. Princeton University Press, Princeton.

Mainwaring, M.C., Lucy, D., Hartley, I.R., 2011. Parentally biased favouritism in relation to offspring sex in zebra finches. Behavioral Ecology and Sociobiology 65, 2261–2268.

Marra, P.P., Holmes, R.T., 2001. Consequences of dominance-mediated habitat segregation in American redstarts during the nonbreeding season. Auk 118, 92–104.

Martin, T.E., 1987. Food as a limit in breeding birds: a life-history perspective. Annual Review of Ecology and Systematics 18, 453–487.

McClelland, G.T.W., Cooper, J., Chown, S.L., 2013. Evidence of breeding by diving petrels and storm petrels at Marion Island after the eradication of feral cats. Ornithological Observations 4, 90–93.

Melbourne, B. a, Hastings, A., 2008. Extinction risk depends strongly on factors contributing to stochasticity. Nature 454, 100–103.

Milazzo, M., Mirto, S., Domenici, P., Gristina, M., 2013. Climate change exacerbates interspecific interactions in sympatric coastal fishes. Journal of Animal Ecology 82, 468–477.

Morin, M., Conant, S., 1998. Laysan Island ecosystem restoration plan. Unpublished report for the U.S. Fish and Wildlife Service. University of Hawaii at Manoa, Honolulu.

Morris, W.F., Doak, D.F., 2002. Quantitative conservation biology. Sinauer Associates Inc., Sunderland, MA.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

Nager, R.G., Monaghan, P., Houston, D.C., Genovart, M., 2000. Parental condition, brood sex ratio and differential young survival: an experimental study in gulls (*Larus fuscus*). Behavioral Ecology and Sociobiology 48, 452–457.

Nagy, K.A., 1987. Field metabolic rate and food requirement scaling in mammals and birds. Ecological Monographs 57, 111–128.

Nagy, K.A., Girard, I.A., Brown, T.K., 1999. Energetics of free-ranging mammals, reptiles, and birds. Annual Review of Nutrition 19, 247–77.

Newson, S.E., Woodburn, R.J.W., Noble, D.G., Baillie, S.R., Gregory, Richard, D., 2005. Evaluating the Breeding Bird Survey for producing national population size and density estimates. Bird Study 52, 42–54.

Newton, I., Dale, L., 2001. A comparative analysis of the avifaunas of different zoogeographical regions. Journal of Zoology 254, 207–218.

Norberg, J., Urban, M.C., Vellend, M., Klausmeier, C.A., Loeuille, N., 2012. Eco-evolutionary responses of biodiversity to climate change. Nature Climate Change 2, 1–5.

O'Dowd, D.J., Green, P.T., Lake, P.S., 2003. Invasional "meltdown" on an oceanic island. Ecology Letters 6, 812–817.

Oddie, K., 1998. Sex discrimination before birth. Trends in Ecology and Evolution 13, 130–131.

Øigarden, T., Lifjeld, J.T., 2012. Primary sex ratios vary with clutch size in the size-dimorphic white-throated dipper *Cinclus cinclus*. Journal of Ornithology 154, 91–97.

Petchey, O.L., McPhearson, P.T., Casey, T.M., Morin, P.J., 1999. Environmental warming alters food-web structure and ecosystem function. Nature 402, 69–72.

Pike, T.W., Petrie, M., 2003. Potential mechanisms of avian sex manipulation. Biological Reviews 78, 553–574.

Pimm, S.L., Jones, H.L., Diamond, J., 1988. On the risk of extinction. American Naturalist 132, 757–785.

Pradel, R., Hines, J.E., Lebreton, J., Nichols, J.D., 1997. Capture-recapture survival models taking account of transients. Biometrics 53, 60–72.

Pulliam, H.R., 1988. Sources, sinks, and population regulation. American Naturalist 132, 652–661.

Purvis, A., Gittleman, J.L., Cowlishaw, G., Mace, G.M., 2000. Predicting extinction risk in declining species. Proceedings of the Royal Society B 267, 1947–1952.

Pütz, K., Clausen, A.P., Huin, N., Croxall, J.P., 2003. Re-evaluation of historical rockhopper penguin population data in the Falkland Islands. Waterbirds 26, 169–175.

R Development Core Team, 2010. R: A language and environment for statistical computing. http://www.r-project.org.

Rankin, D.J., Kokko, H., 2007. Do males matter? The role of males in population dynamics. Oikos 116, 335–348.

Van Rensburg, P.J.J., Bester, M.N., 1988. The effect of cat *Felis catus* predation on three breeding Procellariidae species on Marion Island. South African Journal Of Zoology 23, 301–305.

Van Riper, C.I., 1991. The impact of introduced vectors and avian malaria on insular passeriform bird populations in Hawaii. Bulletin of the Society for Vector Ecology 16, 59–83.

Robertson, A.W., Kelly, D., Ladley, J.J., Sparrow, A.D., 1999. Effects of pollinator loss on endemic New Zealand mistletoes (Loranthaceae). Conservation Biology 13, 499–508.

le Roux, P.C., McGeoch, M.A., 2008a. Changes in climate extremes, variability and signature on sub-Antarctic Marion Island. Climatic Change 86, 309–329.

le Roux, P.C., McGeoch, M.A., 2008b. Rapid range expansion and community reorganization in response to warming. Global Change Biology 14, 2950–2962.

Rowe-Rowe, D.T., Green, B., Crafford, J.E., 1989. Estimated impact of feral house mice on Sub-Antarctic invertebrates at Marion Island. Polar Biology 9, 457–460.

Ruffino, L., Bourgeois, K., Vidal, E., Icard, J., Torre, F., Legrand, J., 2008. Introduced predators and cavity-nesting seabirds: unexpected low level of interaction at breeding sites. Canadian Journal of Zoology 86, 1068–1073.

Ryan, P.G., Bester, M.N., 2008. Pelagic predators, in: Chown, S.L., Froneman, P.W. (Eds.), The Prince Edward Islands: Land-sea Interactions in a Changing Ecosystem. Sun Press, Stellenbosch, pp. 121–164.

Ryan, P.G., Whittington, P.A., Crawford, R.J.M., 2009. A tale of two islands: contrasting fortunes for Subantarctic skuas at the Prince Edward Islands. African Journal of Marine Science 31, 431–437.

Sadler, J.P., 1996. Biodiversity on oceanic islands: a palaeoecological assessment. Journal of Biogeography 26, 75–87.

Savidge, J.A., 1987. Extinction of an island forest avifauna by an introduced snake. Ecology 68, 660–668.

Schamber, J.L., Esler, D., Flint, P.L., 2009. Evaluating the validity of using unverified indices of body condition. Journal of Avian Biology 40, 49–56.

Schluter, D., 2000. The ecology of adaptive radiation. Oxford University Press, Oxford.

Schoen, R., 1983. Measuring the tightness of a marriage squeeze. Demography 20, 61–78.

Schoener, T.W., Spiller, D.A., 1999. Indirect effects in an experimentally staged invasion by a major predator. American Naturalist 153, 347–358.

Schramm, M., 1986. Burrow densities and nest site preferences of petrels (Procellariidae) at the Prince Edward Islands. Polar Biology 6, 63–70.

Shenk, T.M., White, G.C., Burnham, K.P., 1998. Sampling-variance effects on detecting density dependence from temporal trends in natural populations. Ecological Monographs 68, 445–463.

Siegel, V., 2005. Distribution and population dynamics of *Euphausia superba*: summary of recent findings. Polar Biology 29, 1–22.

Smith, V.R., Avenant, N.L., Chown, S.L., 2002. The diet and impact of house mice on a sub-Antarctic island. Polar Biology 25, 703–715.

Spielman, D., Brook, B.W., Frankham, R., 2004. Most species are not driven to extinction before genetic factors impact them. Proceedings of the National Academy of Sciences of the U.S.A. 101, 15261–15264.

Steadman, D.W., 1995. Prehistoric extinctions of Pacific island birds: biodiversity meets zooarchaeology. Science 267, 1123–1131.

Stearns, S.C., 1992. The evolution of life histories. Oxford University Press, Oxford, UK.

Szabo, J.K., Khwaja, N., Garnett, S.T., Butchart, S.H.M., 2012. Global patterns and drivers of avian extinctions at the species and subspecies level. PloS one 7, e47080.

Takimoto, G., Spiller, D.A., Post, D.M., 2008. Ecosystem size, but not disturbance, determines food-chain length on islands of the Bahamas. Ecology 89, 3001–3007.

Thompson, W.L., White, G.C., Gowan, C., 1998. Monitoring vertebrate populations. Academic Press, San Diego.

Towns, D.R., Atkinson, I.A.E., Daugherty, C.H., 2006. Have the harmful effects of introduced rats on islands been exaggerated? Biological Invasions 8, 863–891.

Traill, L.W., Brook, B.W., Frankham, R.R., Bradshaw, C.J.A., 2010. Pragmatic population viability targets in a rapidly changing world. Biological Conservation 143, 28–34.

Trivers, R.L., Willard, D.E., 1973. Natural selection of parental ability to vary the sex ratio of offspring. Science 179, 90–92.

Tylianakis, J.M., Didham, R.K., Bascompte, J., Wardle, D.A., 2008. Global change and species interactions in terrestrial ecosystems. Ecology Letters 11, 1351–1363.

Tylianakis, J.M., Tscharntke, T., Lewis, O.T., 2007. Habitat modification alters the structure of tropical host-parasitoid food webs. Nature 445, 202–205.

Urban, M.C., Tewksbury, J.J., Sheldon, K.S., 2012. On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. Proceedings of the Royal Society B 279, 2072–2080.

Vié, J.-C., Hilton-Taylor, C., Stuart, S.N., 2008. Wildlife in a changing world: an analysis of the 2008 IUCN Red List of Threatened Species. IUCN, Gland, Switzerland.

Walther, G., Post, E., Convey, P., Menzel, A., Parmesank, C., Beebee, T.J.C., Fromentin, J., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. Nature 416, 389–395.

Walther, G.-R., Roques, A., Hulme, P.E., Sykes, M.T., Pysek, P., Kühn, I., Zobel, M., Bacher, S., Botta-Dukát, Z., Bugmann, H., Czúcz, B., Dauber, J., Hickler, T., Jarosík, V., Kenis, M., Klotz, S., Minchin, D., Moora, M., Nentwig, W., Ott, J., Panov, V.E., Reineking, B., Robinet, C., Semenchenko, V., Solarz, W., Thuiller, W., Vilà, M., Vohland, K., Settele, J., 2009. Alien species in a warmer world: risks and opportunities. Trends in Ecology and Evolution 24, 686–693.

Wanless, R.M., Angel, A., Cuthbert, R.J., Hilton, G.M., Ryan, P.G., 2007. Can predation by invasive mice drive seabird extinctions? Biology Letters 3, 241–244.

Warton, D.I., Hui, F.K.C., 2011. The arcsine is asinine: the analysis of proportions in ecology. Ecology 92, 3–10.

Watkins, B.P., Cooper, J., 1986. Introduction, present status and control of alien species at the Prince Edward Islands, sub-Antarctic. South African Journal of Antarctic Research 16, 86–94.

Wegge, P., 1980. Distorted sex ratio among small broods in a declining capercaillie population. Ornis Scandinavica 11, 106–109.

West, S.A., 2009. Sex allocation. Princeton University Press, Princeton.

West, S.A., Reece, S.E., Sheldon, B.C., 2002. Sex ratios. Heredity 88, 117–124.

West, S.A., Sheldon, B.C., 2002. Constraints in the evolution of sex ratio adjustment. Science 295, 1685–1688.

White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:S1, S120:S139.

Whittaker, R.J., Fernández-Palacios, J.M., 2007. Island biogeography. Ecology, evolution and conservation. Oxford University Press, Oxford, UK.

Wikelski, M., Foufopoulos, J., Vargas, H., Snell, H., 2004. Galápagos birds and diseases: Invasive pathogens as threats for island species. Ecology and Society 9, 1–5.

Williams, T.D., Cooch, E.G., Jefferies, R.L., Cooke, F., 1993. Environmental degradation, food limitation and reproductive output: juvenile survival in lesser snow geese. Journal of Animal Ecology 62, 766–777.

Wilson, K., Hardy, I.C.W., 2002. Statistical analysis of sex ratios: an introduction, in: Sex Ratios: Concepts and Research Methods. Cambridge University Press, Cambridge, pp. 48–92.

Winkler, D.W., 1985. Factors determining a clutch size reduction in California gulls (*Larus californicus*): a multi-hypothesis approach. Evolution 39, 667–677.

Winkler, D.W., Walters, J.R., 1983. The determination of clutch size in precocial birds. Current Ornithology 1, 33–68.

Zarnetske, P.L., Skelly, D.K., Urban, M.C., 2012. Biotic multipliers of climate change. Science 336, 1516–1518.

Tables

Table 1: Sheathbill use of foraging habitat used in the east area on Marion Island, 1976-77 and 2008-11. Values are the mean number and proportion of each study area's population (± SD).

Habitat and Season	Number					Proportion			
Winter (May-October)	1976-77	2008-11	*t*	*df*	*p*	1976-77	2008-11	*w*	*p*
King penguin colonies	32.1 ± 10.9	56.4 ± 11.0	-7.341	33.1	<0.001	15.6 ± 6.4	43.6 ± 9.1	6	<0.001
Rockhopper penguin colonies	13.9 ± 8.1	4.0 ± 6.2	4.339	26.4	<0.001	6.9 ± 5.0	10.5 ± 11.4		ns
Intertidal zone	71.1 ± 43.2	71.8 ± 28.8			ns	33.3 ± 17.2	36.8 ± 17.9		ns
Biotic vegetation	59.3 ± 25.9	11.0 ± 11.5	7.308	19.5	<0.001	27.5 ± 11.3	4.7 ± 4.5	516	<0.001
Mire	23.9 ± 27.0	0.9 ± 2.8	3.495	16.2	<0.01	10.7 ± 11.9	0.4 ± 0.9	504	<0.001
Saltspray	13.1 ± 9.6	5.0 ± 4.0	3.342	19.1	<0.01	6.0 ± 4.1	3.3 ± 2.7	375	0.02
Slope	0.2 ± 0.4	1.6 ± 2.9	-2.667	32.0	0.01	0.1 ± 0.2	0.6 ± 1.3		ns
Summer (November-April)									
King penguin colonies	60.9 ± 11.8	58.3 ± 9.9			ns	34.1 ± 6.1	45.3 ± 9.6	96	<0.001
Rockhopper penguin colonies	68.9 ± 22.8	22.3 ± 11.8	7.923	20.4	<0.001	39.0 ± 13.0	12.9 ± 12.8	529	<0.001
Intertidal zone	28.4 ± 22.0	25.6 ± 12.8			ns	15.4 ± 10.9	30.1 ± 15.1	124	0.001
Biotic vegetation	12.2 ± 11.1	3.8 ± 4.0	3.018	18.1	<0.01	6.9 ± 6.6	5.2 ± 6.1		ns*
Mire	4.0 ± 2.8	2.0 ± 3.7	2.148	41.0	0.04	2.2 ± 1.4	2.0 ± 3.5	410	0.01
Saltspray	4.2 ± 3.2	3.7 ± 3.3			ns	2.3 ± 1.8	3.2 ± 2.8		ns
Slope	0.2 ± 0.4	1.2 ± 2.5	-2.326	36.1	0.03	0.1 ± 0.2	1.2 ± 2.1		ns

*Two-sample *t*-test found a significant difference; $t = 2.02$, $df = 45.1$, $p = 0.049$.

Table 2: Change in available energy (kJ ha^{-1}) in the form of macroinvertebrates and the amount collectively removed by invasive mice in the mire and biotic habitats during the winter season (May to October) on Marion Island. Note that years between estimates of available macroinvertebrate energy and removal by mice differ.

Available monthly macroinvertebrate energy (kJ ha^{-1})

	Mire	Biotic
1976-77	963 363 ± 1 259 074	6 767 924 ± 3 618 692
1996-97	115 668 ± 113 824	3 007 572 ± 1 502 746
2006-07	32 777 ± 63 948	1 101 174 ± 795 546

Estimated monthly energy collectively removed by invasive mice (kJ ha^{-1})

	Mire	Biotic
1979-80	29 049 ± 20 601	131 409 ± 56 922
1993-94	85 330 ± 20 353	99 850 ± 19 975
2008-11	212 132 ± 132 977	125 453 ± 35 659

Table 3: Mean (± SD) masses (g) of breeding sheathbills in 1976-77, 1994-95, and 2008-11 in the east study area on Marion Island.

			Early summer			Late summer			Early winter			Late winter		
		Study	mass	*n*	*p*	mass	*n*	*p*	mass	*n*	*p*	mass	*n*	*p*
Females	RH	1976-77	451.8 (± 34.2)	19	A[a]	443.6 (± 32.9)	17	0.03	450.4 (± 21.6)	13	0.04	460.9 (± 34.6)	9	0.001
		1994-95	426.6 (± 32.2)	19	B									
		2008-11	422.3 (± 22.2)	8	B	420.0 (± 23.0)	12		433.3 (± 18.1)	12		405.4 (± 21.3)	12	
	KP	1976-77	460.5 (± 34.4)	11	ns	475.9 (± 29.0)	7	ns	477.9 (± 39.8)	12	0.05	456.5 (± 19.3)	8	ns
		1994-95												
		2008-11	446.9 (± 32.3)	16		440.0 (± 45.3)	9		450.6 (± 24.1)	18		451.9 (± 35.2)	13	
Males	RH	1976-77	487.0 (± 31.2)	10	ns	504.0 (± 37.3)	13	0.03	529.9 (± 38.4)	17	ns	504.9 (± 22.5)	14	ns
		1994-95	487.7 (± 38.1)	15										
		2008-11	483.3 (± 38.9)	12		475.5 (± 18.3)	10		532.5 (± 28.6)	6		491.3 (± 48.7)	8	
	KP	1976-77	519.6 (± 35.4)	13	ns	540.6 (± 40.9)	18	0.03	539.3 (± 36.8)	11	ns	512.7 (± 33.2)	18	ns
		1994-95												
		2008-11	506.9 (± 20.5)	8		512.4 (± 39.3)	23		547.6 (± 32.5)	18		509.6 (± 32.1)	13	

[a] Tukey's hsd ($p<0.05$), study years labelled with the same letter do not differ significantly

Table 4: Sheathbill counts conducted in the winter (July-September) and summer (November-December) seasons on Marion Island. Summer counts occurred prior to the breeding season.

Year	Season	Count (± SD)	Independent Observers	Source
1976	winter	3602	1	1
1976	summer	3711	1	1
1994	winter	2628	1	1
1994	summer	3236	1	1
1995	winter	3537	1	1
1995	summer	3028	1	1
1996	winter	2850	1	1
1996	summer	2637	1	1
2008	winter	3453 (± 312)	4	2
2009	winter	4042 (± 201)	4	2
2010	winter	4132 (± 274)	3	2
2011	winter	4211 (± 188)	2	2

[1] Huyser et al., (2000)

[2] This study

Table 5: Sheathbill breeding parameters in the east study area on Marion Island, 1973-77, 1994-95, and 2008-11.

Years	Egg Mass (g)					Clutch Size (presented as %)								Productivity (mean fledglings per nest)				
	AVG	*t*	*df*	*p*	*n*	1	2	3	4	*F*	*df*	Tukey hsd[a]	*n*	AVG	*F*	*df*	*p*	*n*
1973-77	41.9 (± 1.9)	4.53	19	ns	26	2.6	47.4	47.4	2.6	14.45	146	A	38	1.07 (± 0.89)	0.48	190	ns	42
1994-95						18.2	72.7	9.1	0.0			B	22	0.92 (± 0.69)				26
2008-11	38.6 (± 2.8)				20	11.4	76.1	12.5	0.0			B	88	0.95 (± 0.70)				123

[a] Tukey's hsd ($p<0.05$), study years labelled with the same letter do not differ significantly.

Table 6: Relationship between habitat, sex ratio, nestling survival and adult female body mass (± SD) on Marion Island, 2010-11. Sex ratio indicates males. Nestling survival refers only to the post-brooding stage.

Sheathbill habitat	Secondary sex ratio	Tertiary sex ratio	Adult female body mass	Male nestling survival	Female nestling survival	*n*
Rockhopper penguin colony	0.292	0.253	430.9 (± 33.5)	78.6 %	95.6 %	92
King penguin colony	0.424	0.364	459.6 (± 34.8)	85.7 %	95.5 %	36

Table 7: Summary of model selection for sheathbill survival on Marion Island. ϕ and p indicate survival rate and recapture rate, respectively. Additive effects are denoted by '+', interactive effects by '*'. Model selection was based on Akaike's Information Criterion adjusted for overdispersion and sample size (QAICc), where a smaller value indicates a better model. ΔQAICc is the difference in QAICc between the current model and the best. QAICc weights give the relative support each model has compared to the others, and K is the number of parameters. QDeviance is the model deviance divided by the variance inflation factor ĉ. Models with ΔQAICc > 7 only are shown.

		Model	QAICc	ΔQAICc	QAICc weights	K	QDeviance
Non-breeding birds	1	ϕ(habitat + study area + age + season + habitat * age * season) p(study area + age + time + study area * time)	2269.290	0	0.244	24	460.498
	2	ϕ(habitat + study area + age + season + habitat * age) p(study area + age + time + study area * time)	2269.624	0.335	0.206	22	460.833
	3	ϕ(habitat + study area + age + season) p(study area + age + time + study area * time)	2269.657	0.367	0.203	20	464.978
	4	ϕ(habitat + study area + age + season + habitat * season) p(study area + age + time + study area * time)	2269.841	0.522	0.185	21	463.107
	5	ϕ(habitat + study area + age + season + age * season) p(study area + age + time + study area * time)	2271.341	2.051	0.087	21	464.607
	6	ϕ(habitat + age + season + habitat * age) p(study area + age + time + study area * time)	2273.912	4.622	0.024	20	469.233
	7	ϕ(habitat + study area + age + season) p(habitat + age + time + habitat * time)	2274.496	5.203	0.018	19	471.867
	8	ϕ(habitat + study area + age + season) p(habitat + age + time)	2275.677	6.387	0.010	15	481.233

Breeding adults	1	ϕ(season) p(habitat + study area + sex + time + sex * time)	891.262	0	0.337	15	214.777
	2	ϕ(.) p(habitat + study area + sex + time + sex * time)	891.580	0.319	0.287	13	219.182
	3	ϕ(season) p(habitat + study area + time)	893.710	2.448	0.099	10	227.418
	4	ϕ(habitat + season) p(habitat + study area + time)	894.418	3.156	0.070	11	226.094
	5	ϕ(season) p(habitat + study area + sex + time)	895.100	3.838	0.049	11	226.776
	6	ϕ(season) p(habitat + site + time + study area * time)	895.373	4.111	0.043	14	220.933
	7	ϕ(habitat + season) p(habitat + study area + sex + time)	895.915	4.654	0.031	12	225.556
	8	ϕ(habitat + season + habitat * season) p(habitat + study area + time)	896.236	4.974	0.028	12	225.876
	9	ϕ(habitat + sex + season) p(habitat + study area + time)	896.424	5.162	0.026	12	226.064
	10	ϕ(habitat + sex + season) p(habitat + study area + sex + time)	897.952	6.690	0.019	13	225.554

Table 8: Estimates of mean sheathbill demographic parameters used in matrix population models. Whole-island estimates of mean fledgling production are weighted according to the proportion of sheathbills in each habitat. Variance for weighted means was calculated using ratio variance approximation (Cochran 1977). ϕ indicates a six-month survival rate; lcl indicates lower 95 % confidence limit; ucl indicates upper 95% confidence limit. Whole-island estimates of mean apparent survival were obtained by constraining survival models to exclude habitat and study area. Estimates of mean apparent survival for RH and KP sheathbills were obtained by constraining survival models to exclude study area.

	Whole-island			RH sheathbills			KP sheathbills		
Starting population values									
Juvenile females				230			100		
Juvenile males				55			80		
Subadult females				180			40		
Subadult males				90			40		
Adult females				1600			200		
Adult males				1300			200		
Reproduction									
Probability of males breeding	0.793								
Estimated available nests				1000			200		
Males fledged per nest	0.24	(±0.04 SD)		0.22	(±0.04 SD)		0.31	(±0.06 SD)	
Females fledged per nest	0.69	(±0.06 SD)		0.67	(±0.13 SD)		0.74	(±0.15 SD)	
Mortality									
	ϕ	lcl	ucl	ϕ	lcl	ucl	ϕ	lcl	ucl
Juvenile survival [a]									

Summer	0.671	0.521	0.822	0.636	0.484	0.765	0.838	0.657	0.933
Winter	0.602	0.414	0.790	0.558	0.454	0.657	0.811	0.677	0.897
Subadult survival									
summer	0.880	0.852	0.908	0.874	0.754	0.940	0.912	0.747	0.973
winter	0.868	0.807	0.928	0.853	0.722	0.929	0.935	0.829	0.977
Breeding adult survival									
summer	0.979	0.955	0.991	0.981	0.954	0.992	0.979	0.953	0.991
winter	0.962	0.930	0.979	0.962	0.930	0.980	0.959	0.916	0.980

Figure Legends

Figure 1: Marion Island showing localities mentioned in the text. Circles indicate the east (green), north (orange) and west (red) study areas.

Figure 2: Life-cycle diagram composed of four groups (male KP sheathbills, female KP sheathbills, male RH sheathbills, and female sheathbills) for Marion Island sheathbills based on a pre-breeding census. Notation includes: ϕ = probability of survival, Ψ = carrying capacity, R = fecundity, and p = sex ratio at fledge. Subscripts include: m = male, f = female, k = KP sheathbills, r = RH sheathbills, 1 = juveniles, 2 = subadults (2 yr-olds), 3 = subadults (3 yr-olds), 4 = adults, w = winter, and s = summer.

Figure 3: a) Mean (± SD) monthly total abundance of sheathbills in the east study area in 1976-77 (black), 1994-95 (red), and 2008-11 (blue) and mean monthly abundances of sheathbills in b) coastal and inland vegetation, c) the intertidal zone, d) rockhopper penguin colonies, and e) king penguin colonies. The vertical dashed grey lines delineate the winter (May-October) and summer (November to April) seasons. Study periods labelled with the same letters do not differ significantly on a seasonal basis (Tukey's hsd, p <0.05, following ANOVA). The high variance for the month of June in 1976-77 in some habitats is due to a survey during heavy snow cover which prevented sheathbills from foraging inland (Burger, 1981a).

Figure 4: Sheathbill projected breeding population sizes over a 300-year time period on Marion Island under current demographic parameters (solid line), a 50 % reduction in RH sheathbill breeding sites (dashed line), and a 75 % reduction in RH sheathbill breeding sites (dotted line). Black lines refer to the absolute population size including juveniles, subadults, and adults. Red and blue lines refer to the number of adult females and males, respectively.

Figure 5: Distribution and habitat use of sheathbills on Marion Island in August 2009 (with Flannery compensation). Abandoned macaroni (the three largest concentrations of sheathbills on the east coast) and rockhopper penguin colonies (the remainder of sheathbills) were combined under "Abandoned Crested Penguin colony".

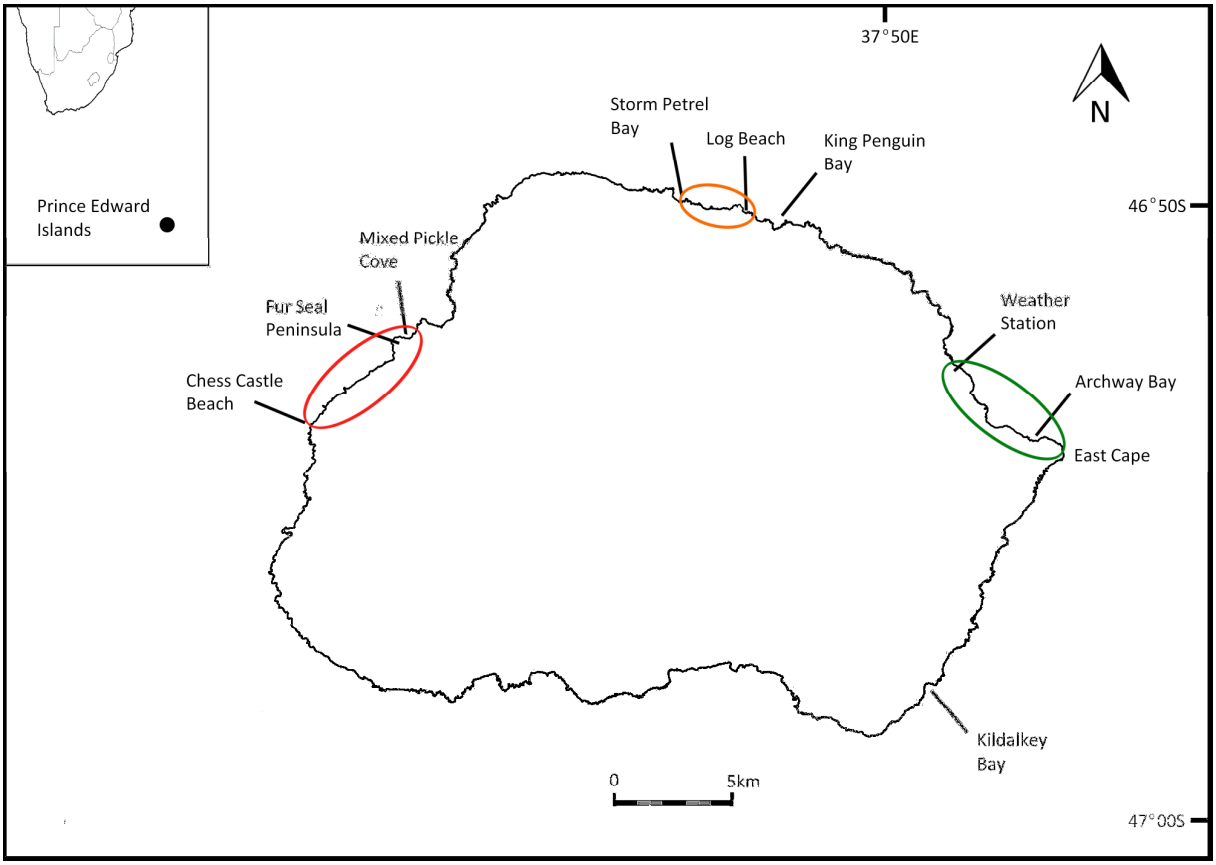


Figure 1

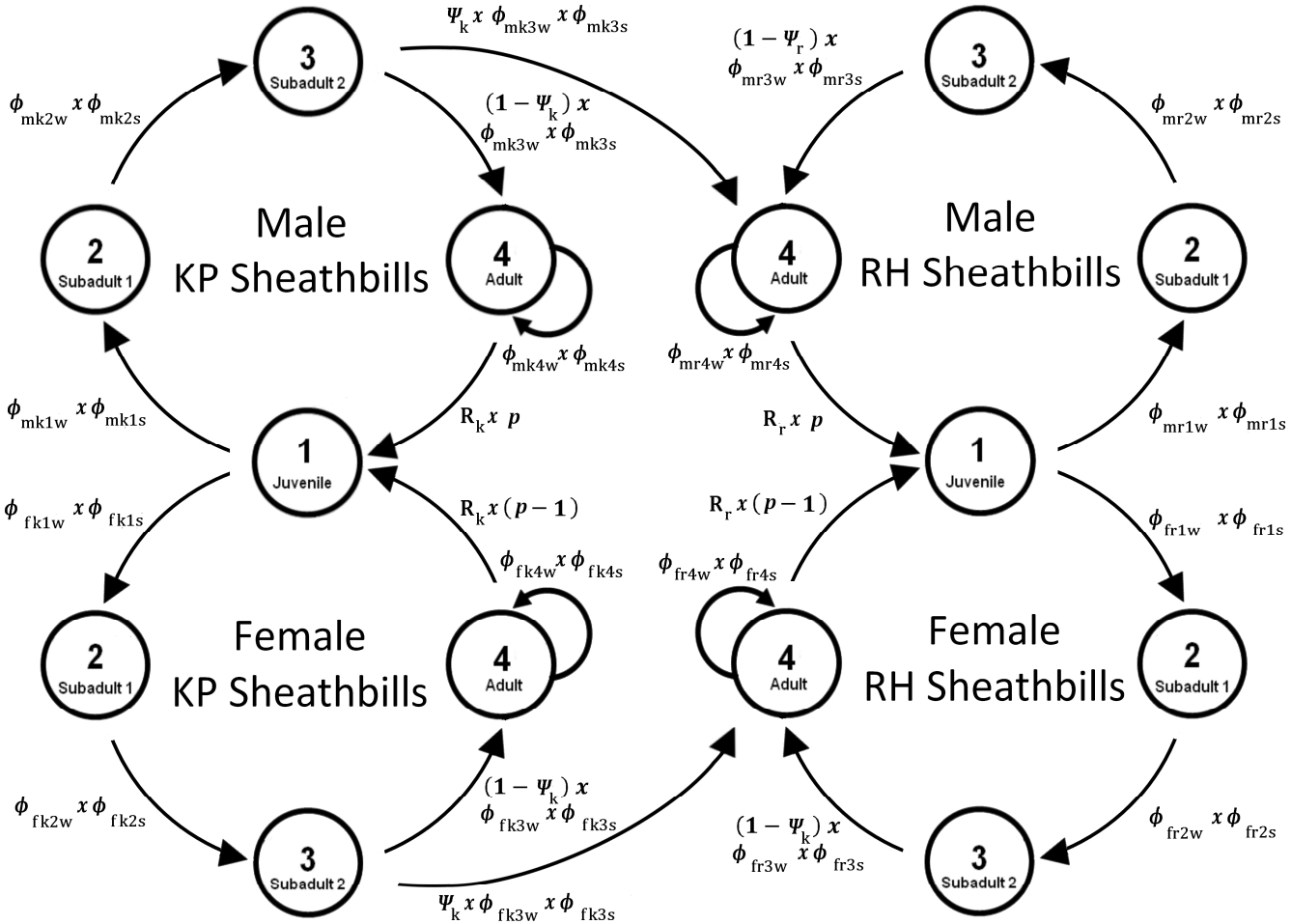


Figure 2

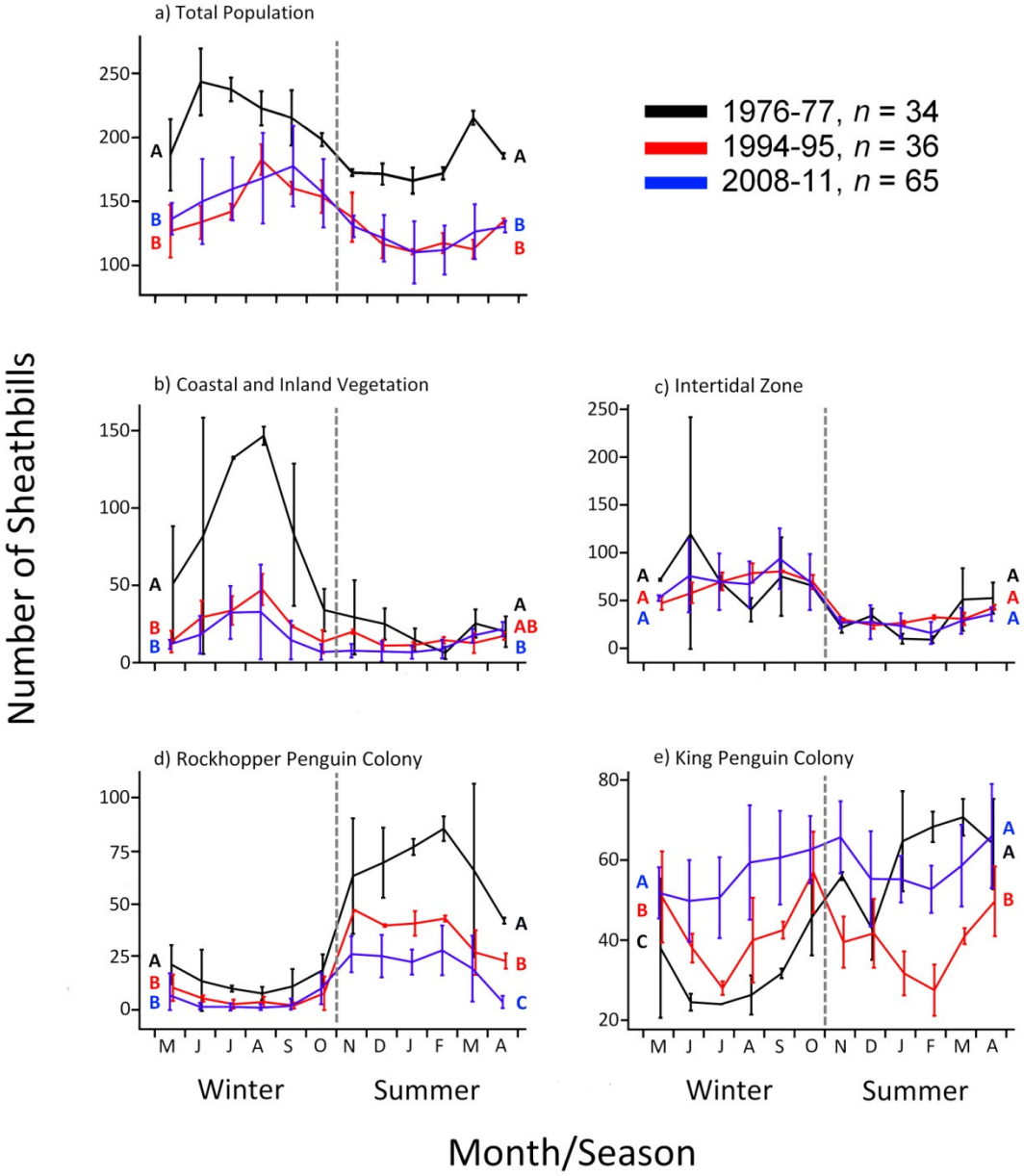


Figure 3

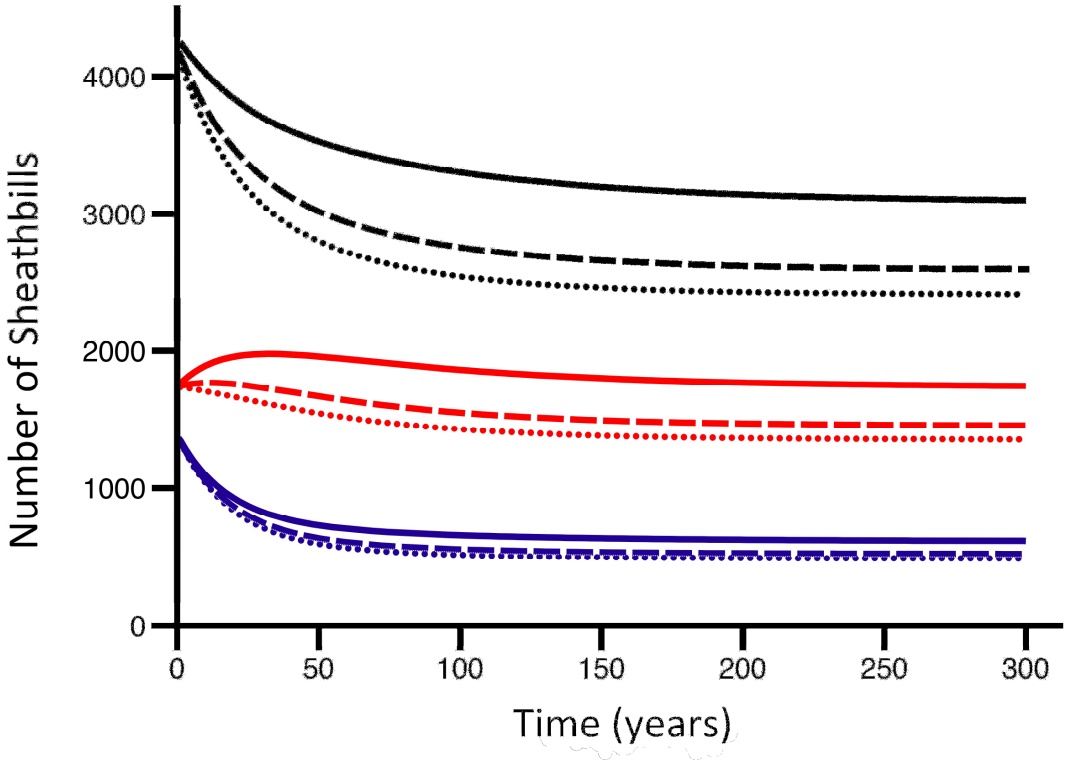


Figure 4

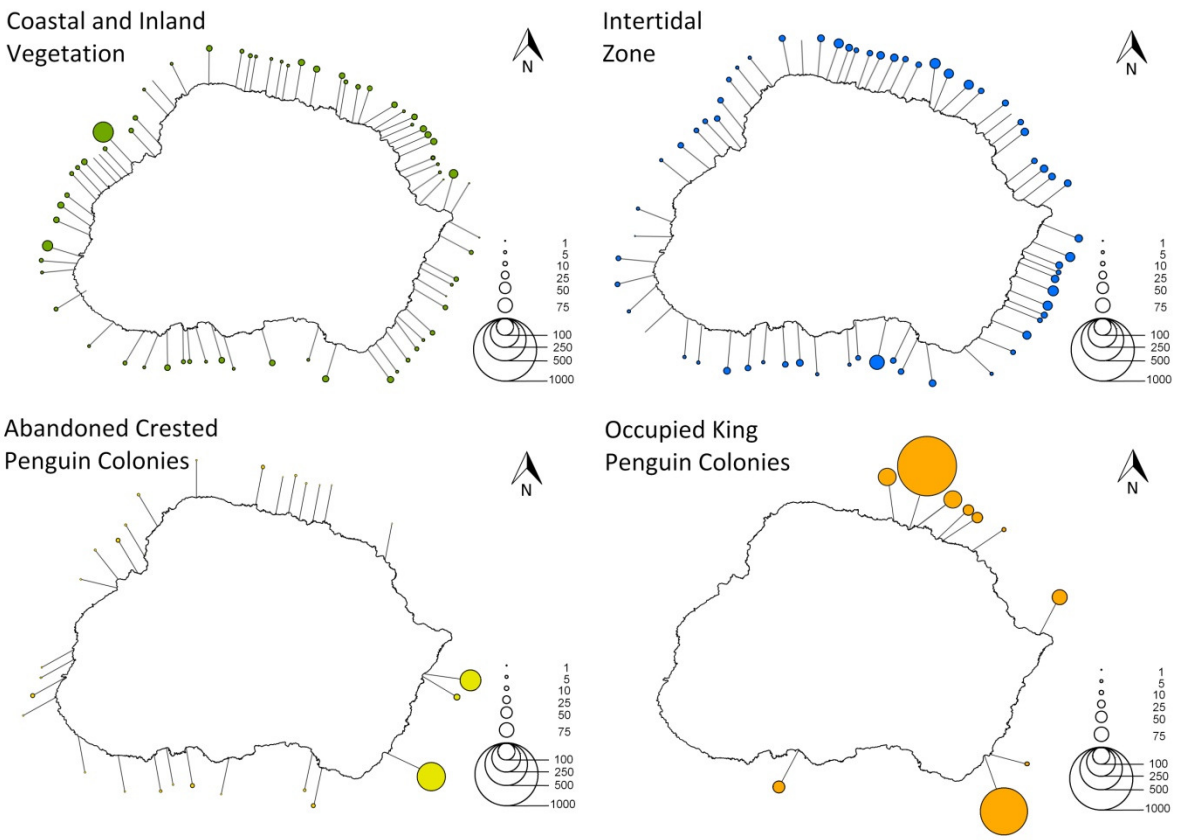


Figure 5

Supplementary Materials

Supplementary Table A1: Shapiro-Wilkes normality test after logit-transformation of the proportion of sheathbills in foraging habitats in the east study area on Marion Island in 1976-77 and 2008-11.

Habitat	Winter		Summer	
	w	*p*	*w*	*p*
King penguin colonies	0.903	0.001	0.990	ns
Rockhopper penguin colonies	0.915	0.002	0.850	<0.001
Intertidal zone	0.986	ns	0.969	ns
Biotic vegetation	0.956	ns	0.962	ns
Mire vegetation	0.778	<0.001	0.858	<0.001
Saltspray vegetation	0.969	ns	0.936	ns
Slope vegetation	0.583	<0.001	0.647	<0.001

Supplementary Table A2: Two sample t-tests of the proportion of sheathbills in foraging habitats in the east study area on Marion Island in 1976-77 and 2008-11 for habitats that were found to have a normal distribution.

Habitat	Winter			Summer		
	t	*df*	*p*	*t*	*df*	*p*
King penguin colonies				-4.835	43.02	<0.001
Rockhopper penguin colonies						
Intertidal zone	-0.382	37.07	ns	-3.793	30.06	0.001
Biotic vegetation	9.526	45.98	<0.001	2.027	45.07	0.049
Mire vegetation						
Saltspray vegetation	2.636	33.73	0.013			
Slope vegetation						

Supplementary Table A3: Mann-Whitney-Wilcoxon test of the proportion of sheathbills in foraging habitats in the east study area on Marion Island in 1976-77 and 2008-11.

Habitat	Winter		Summer	
	w	*p*	*w*	*p*
King penguin colonies	6.0	<0.001	92.5	<0.001
Rockhopper penguin colonies	267.0	ns	529.0	<0.001
Intertidal zone	228.0	ns	124.0	0.001
Biotic vegetation	516.0	<0.001	372.0	ns
Mire vegetation	504.0	<0.001	410.0	0.013
Saltspray vegetation	375.0	0.017	254.5	0.496
Slope vegetation	220.0	ns	210.0	ns

Supplementary Table A4: Mean (± SD) numbers and proportions of sheathbills occurring in different habitats during the winter and summer seasons in the East, North and West study areas at Marion Island, 2008-11. Shaded entries indicate biotic vegetation manured by specific species groups on the island. They are summed and presented as "Biotic vegetation (Total)".

Habitat and Season	Numbers [a]			Proportion		
	East	North	West	East	North	West
Winter (May-October)						
King penguin colonies	56.4 ± 11.0	87.2 ± 14.1	NA	43.6 ± 9.1	60.5 ± 9.8	NA
Rockhopper penguin colonies	4.0 ± 6.2	6.7 ± 5.8	4.5 ± 6.4	10.5 ± 11.4	4.9 ± 4.4	2.5 ± 3.6
Intertidal zone	71.8 ± 28.8	14.0 ± 12.0	90.3 ± 50.4	36.8 ± 17.9	9.3 ± 7.4	53.2 ± 27.2
Biotic vegetation (fur seal)	3.8 ± 5.4	6.2 ± 5.7	31.3 ± 30.8	2.4 ± 3.5	4.3 ± 4.2	16.4 ± 13.9
Biotic vegetation (petrel spp)	0.3 ± 0.6	0.9 ± 2.0	3.2 ± 7.4	0.2 ± 0.4	0.5 ± 1.3	1.8 ± 4.3
Biotic vegetation (albatross spp)	0.1 ± 0.3	0.8 ± 2.1	1.0 ± 1.6	0.1 ± 0.2	0.5 ± 1.3	0.6 ± 0.9
Biotic vegetation (Crozet shag)	0.9 ± 1.0	0.8 ± 1.1	1.6 ± 2.2	0.7 ± 0.8	0.5 ± 0.8	1.0 ± 1.4
Biotic vegetation (gentoo penguin)	1.7 ± 3.3	0.7 ± 1.5	NA	1.0 ± 1.9	0.5 ± 1.0	NA
Biotic vegetation (unknown)	4.2 ± 10.5	5.5 ± 11.6	0.7 ± 1.4	2.5 ± 5.6	3.2 ± 6.3	2.1 ± 7.8
Biotic vegetation (Total)	11.0 ± 11.5	14.8 ± 12.2	37.9 ± 32.9	4.7 ± 4.5	9.6 ± 6.9	21.8 ± 16.6
Mire vegetation	0.9 ± 2.8	3.9 ± 6.8	2.0 ± 2.6	0.4 ± 0.9	2.5 ± 4.0	1.2 ± 1.8
Saltspray vegetation	5.0 ± 4.0	17.4 ± 11.2	34.2 ± 31.8	3.3 ± 2.7	11.5 ± 6.8	19.6 ± 17.3
Slope vegetation	1.6 ± 2.9	2.9 ± 3.8	3.1 ± 6.6	0.6 ± 1.3	1.9 ± 2.3	1.6 ± 3.0
Summer (November-April)						
King penguin colonies	58.3 ± 9.9	80.1 ± 15.9	NA	45.3 ± 9.6	53.1 ± 8.3	NA
Rockhopper penguin colonies	22.3 ± 11.8	38.5 ± 15.5	92.6 ± 36.1	12.9 ± 12.8	26.2 ± 11.7	50.3 ± 21.0
Intertidal zone	25.6 ± 12.8	10.4 ± 10.0	68.6 ± 35.2	30.1 ± 15.1	6.4 ± 5.7	34.7 ± 14.1
Biotic vegetation (fur seal)	2.2 ± 3.4	3.2 ± 4.5	11.8 ± 19.4	1.8 2.7	2.1 ± 3.0	5.5 ± 8.9
Biotic vegetation (petrel spp)	0.2 ± 0.9	0.3 ± 0.7	0.6 ± 1.2	0.2 0.8	0.2 ± 0.5	0.3 ± 0.7
Biotic vegetation (albatross spp)	0.0 ± 0.2	0.1 ± 0.4	0.1 ± 0.3	0.0 0.2	0.1 ± 0.2	0.0 ± 0.2

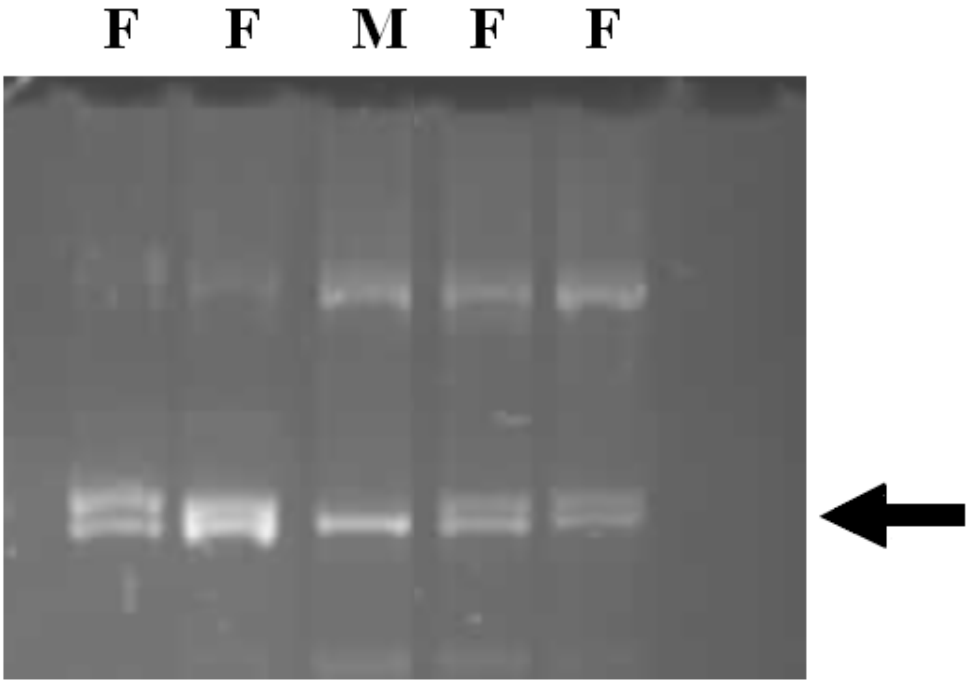
Biotic vegetation (Crozet shag)	0.3	±	0.7	0.4	±	0.9	0.7	±	1.4	0.3	0.5	0.2	±	0.6	0.4	±	0.7
Biotic vegetation (gentoo penguin)	0			0.1	±	0.2	NA			0		0.0	±	0.2	NA		
Biotic vegetation (unknown)	1.0	±	1.8	0.4	±	2.0	1.5	±	5.4	0.8	1.5	0.2	±	1.1	1.4	±	5.8
Biotic vegetation (Total)	3.8	±	4.0	2.2	±	5.9	1.7	±	5.1	5.2	± 6.1	1.5	±	3.7	1.4	±	5.0
Mire vegetation	2.0	±	3.7	5.4	±	8.4	1.3	±	2.6	2.0	± 3.5	3.0	±	4.6	0.6	±	1.2
Saltspray vegetation	3.7	±	3.3	10.7	±	8.4	10.9	±	10.8	3.2	± 2.8	7.0	±	5.5	5.3	±	4.5
Slope vegetation	1.2	±	2.5	4.5	±	4.8	14.7	±	19.3	1.2	± 2.1	2.9	±	3.3	7.6	±	9.8

[a] Sample sizes (number of surveys) are as follows: East winter *n* = 30, East summer *n* = 34, North winter *n* = 28, North summer *n* = 31, West winter *n* = 23, West summer *n* = 29.

Supplementary Table A5: Mean (± SD) numbers and proportion of sheathbills occurring in different habitats on Marion Island, 2008-11, based on winter (August-September) surveys. Shaded entries indicate biotic vegetation manured by specific species groups on the island. They are summed and presented as "Biotic vegetation (Total)".

Habitat	Numbers [a]								Proportion							
	2008		2009		2010		2011		2008		2009		2010		2011	
King penguin colonies	1498.5	± 136.5	1727.0	± 76.5	1807.5	± 7.8	1446.0	± 48.1	40.6	± 2.5	42.8	± 1.1	45.5	± 1.1	37.4	± 3.7
Rockhopper penguin colonies	96.0	± 36.8	86.5	± 14.3	18.0	± 22.6	80.5	± 13.4	2.6	± 1.0	2.1	± 0.3	0.5	± 0.6	2.1	± 0.5
Macaroni penguin colonies	368.5	± 24.7	292.0	± 48.9	235.0	± 79.2	408.5	± 13.4	10.1	± 0.6	7.2	± 0.8	5.9	± 2.1	10.5	± 0.4
Intertidal zone	785.5	± 33.2	1012.5	± 45.5	1407.0	± 28.3	845.5	± 187.4	21.3	± 0.4	25.1	± 0.5	35.4	± 1.4	21.7	± 3.4
Biotic vegetation (fur seal)	302.0	± 0.0	297.3	± 29.6	53.5	± 27.6	157.0	± 15.6	8.2	± 0.2	7.3	± 0.5	1.3	± 0.7	4.1	± 0.7
Biotic vegetation (petrel spp)	236.5	± 3.5	63.8	± 6.8	15.0	± 21.2	29.5	± 2.1	6.4	± 0.1	1.6	± 1.0	0.4	± 0.5	0.8	± 0.0
Biotic vegetation (albatross spp)	24.5	± 3.5	12.3	± 3.4	11.5	± 2.1	55.5	± 0.7	0.7	± 0.1	0.3	± 0.1	0.3	± 0.1	1.4	± 0.1
Biotic vegetation (Crozet shag)	30.5	± 27.6	40.3	± 3.2	34.0	± 1.4	0		0.8	± 0.8	1.0	± 0.0	0.9	± 0.0	0	
Biotic vegetation (gentoo penguin)	24.0	± 12.0	55.0	± 7.8	27.0	± 8.5	49.0	± 7.1	0.7	± 0.0	1.4	± 0.2	0.7	± 0.2	1.3	± 0.1
Biotic vegetation (unknown)	20.5	± 9.2	4.0	± 2.0	30.0	± 4.2	42.0	± 9.9	0.6	± 0.3	0.0	± 0.0	0.8	± 0.1	1.1	± 0.2
Biotic vegetation (Total)	638.0	± 43.8	472.5	± 50.8	171.0	± 65.1	333.0	± 35.4	17.3	± 1.5	11.6	± 1.0	4.3	± 1.6	8.6	± 1.0
Mire vegetation	47.5	± 19.1	18.0	± 7.1	19.5	± 26.2	90.0	± 17.0	1.3	± 0.6	0.5	± 0.2	0.5	± 0.7	2.3	± 0.3
Saltspray vegetation	170.5	± 9.2	259.0	± 31.2	235.0	± 169.7	404.0	± 46.7	4.6	± 0.4	5.9	± 0.9	5.9	± 3.8	10.4	± 0.5
Slope vegetation	61.5	± 4.9	161.8	± 25.6	5.0	± 4.2	235.5	± 38.9	1.7	± 0.2	4.0	± 0.6	0.1	± 0.1	6.1	± 0.6
Fjaeldmark vegetation	16.5	± 9.2	1.5	± 1.7	0		34.0	± 5.7	0.4	± 0.2	0.0	± 0.0	0		0.9	± 0.1

[a] Sample sizes (number of independent surveyors) are as follows: 2008 *n* = 2, 2009 *n* = 4, 2010 *n* = 2, 2011 *n* =2.



Supplementary Figure A1: The sex of five individual sheathbill chicks on Marion Island as indicated by the number of bands resolved on agarose gel. The arrow indicates bands specific to sex determination. “M” and “F” indicate male and female birds, respectively.

Chapter 4 – The basal metabolic rate of black-faced sheathbills (*Chionis minor*) on Marion Island, sub-Antarctic

"At the rookery, these birds were living on all sorts of filth dropped by the penguins, and were the scavengers of the place" **– H.N. Mosely, Marion Island, 1879**

A black-faced sheathbill (*Chionis minor marionensis*), surveys its territory at Archway Bay King Penguin Colony, Marion Island

Introduction

Basal metabolic rate (BMR) is a fundamental characteristic of all endotherms. It accounts for upwards of 40-50% of the total daily energy budget in free-living animals (Bryant, 1997; Speakman, 2000) and underlies all processes contributing to a species' ecology including behaviour, distribution, and life history (Brown et al., 2004; White, Cassey, et al., 2007; Biro and Stamps, 2010). In turn, BMR is influenced most significantly by body mass and temperature (Krogh, 1914; White, Blackburn, et al., 2007; Clarke et al., 2010; White and Kearney, 2012), but also shows substantial residual variation. This residual variation has phylogenetic (Hayssen and Lacy, 1985; Kozlowski and Konarzewski, 2004), ecological (Lovegrove, 2000; McNab, 2003a, 2009) and geographic (McNab, 2002; Wikelski et al., 2003; White et al., 2011) components.

Understanding the scope of variation in any higher taxon is significant for comprehending its full implications in shaping ecological patterns and processes. For example, diversification rate in birds appears to be related to clade body size in birds, with smaller-bodied clades diversifying more rapidly. However, this effect is largely non-significant within the passerines (Phillimore et al., 2006), suggesting that size-related differences in diversification rate may have most to do with differences between passerines and non-passerines. In much the same way, missing taxa or the exclusion of them could obscure signal in the evolution of a wide variety of traits (Bininda-Edmonds and Gittleman, 2000; Bininda-Edmonds, 2004). For BMR, species or groups that are phylogenetically or ecologically distinct often have metabolic rates beyond the norm (McNab, 1995, 1996; Bozinovic et al., 2004). Indeed, McNab (1992) pointed out that the number of factors associated with BMR significantly increases as the number of species and the ecological diversity of the assemblage increases. For BMR in birds, many taxa have been investigated, and often comprehensively (McKechnie and Wolf, 2004; Jetz et al., 2008; McNab, 2009). However, several significant clades have not been investigated. Many of these are unusually placed on bird phylogeny, are restricted to islands, or have unusual life histories. In consequence, they might be expected to add substantial variation (McNab, 1992; White et al., 2012), and this idea should at least be tested.

A further factor that may complicate the investigation of the way BMR and other traits influence community patterns, an approach growing in significance in ecology (Weiher and Keddy, 1995; Kraft et al., 2007; Webb et al., 2010) is intraspecific variation in these traits (Jung et al., 2010). It is becoming increasingly recognized that mean species trait values are less than ideal when attempting to understand the processes by which local communities are assembled (Araújo et al., 2011; Bolnick et al., 2011; Violle et al., 2012) and that many broad-scale patterns and processes, from food web structure (Melian et al., 2011) to ecosystem functioning (Madritch and Hunter, 2002), are influenced at an individual level. Indeed, it has been widely recognized that such variation can affect the way assemblages are structured and several ways to deal with it have been proposed (Gotelli et al., 2009; Chown et al., 2010). Understanding the scope of this variation is therefore important both for a fundamental understating of BMR evolution (Wikelski et al., 2003; Broggi et al., 2005; Tieleman et al., 2009; Konarzewski and Książek, 2012) and for understanding the way assemblages are structured.

Here, both of these important sources of BMR variation are addressed by investigating the BMR of the black-faced sheathbill (*Chionis minor* Hartlaub) on sub-Antarctic Marion Island. The family Chionididae is phylogenetically distinct, serving as an intermediate form of the more typical Charadriiformes (Livezey, 2010). Occurring exclusively on several archipelagos in the southern Indian Ocean, sheathbills are members of the small ecological group of high latitude island endemic birds. Latitude (Weathers, 1979; Wiersma et al., 2007) and island endemism (McNab, 2002; McNab and Ellis, 2006) have both been identified as important forces in shaping a species' energetics, yet to date measurements from this group have been limited to a small sample of captive birds (McNab and Salisbury, 1995; McNab, 2003b).

Marion Island sheathbills are also well suited for examining intraspecific variation. Though all sheathbills can be described as opportunistic omnivores, the population can be divided into two distinct and sympatric groups. One group (hereafter referred to as KP sheathbills) forages year-round in continuously occupied king penguin (*Aptenodytes patagonicus* Miller) colonies where they consume mostly the stomach contents of penguins obtained through kleptoparasitism, penguin carcasses, and excreta (Burger, 1984). The second group (hereafter referred to as RH sheathbills) occupies eastern rockhopper penguin

(*Eudyptes chrysocome filholi* Hutton) colonies during their breeding season and their diet is similar to that of KP sheathbills during this period (Burger 1981; Burger 1984). However, when rockhopper penguins leave the island after their five-month breeding season, RH sheathbills are forced to forage elsewhere for the remainder of the year. Many of these birds would traditionally forage for terrestrial invertebrates, but competition with invasive mice has lowered prey abundance to the point of dietary insignificance (Chapter 3, Huyser et al., 2000). The majority of RH sheathbills currently forage in the intertidal zone where they focus on polychaete worms. Switching between the two foraging groups is rare and most birds employ only one strategy once they reach breeding age and establish a breeding territory. In addition, the two sheathbill groups differ in body size, clutch size, chick production, and behaviour (Chapter 3). Because many territory-holding adults rarely travel more than 200 m afield, some birds conceivably live beyond two decades within a few hundred meters of one another yet experience a disparate life history. Thus, sheathbills are well positioned to offer insight into the causes and consequences of intraspecific variation in BMR.

Thus, this study had three major aims. First, to document the BMR of black-faced sheathbills on Marion Island. Second, to determine whether the phylogenetic position and ecology of sheathbills equate to a unique BMR when allometrically compared to other birds. Third, to quantify the variability in sheathbill BMR and identify possible sources and implications of any variation found.

Methods

Study site and animal capture

This study took place on sub-Antarctic Marion Island (46°54'S 37°45'E). The island is situated to the north of the Antarctic Polar Front and together with smaller Prince Edward Island, makes up the Prince Edward Island group. Marion has an area of 290 km^2 and a total coastline of 72 km. The island's climate is best described as oceanic, characterized by strong winds, high humidity, and rainfall (Smith, 2002). There is low daily temperature variation and mean monthly temperatures range between 3° (September) and 8.5° C (February; le Roux 2008). A comprehensive overview of the biology, geology, and climate of the Prince Edward Islands is provided by Chown and Froneman (2008)

Measurements took place from April to May 2011, several weeks after the sheathbill breeding season and the start of winter foraging behaviour. Sheathbills were captured within a 5 km area east of the research station (Fig. 1). All individuals were selected from a long-term study population and only adults that had bred or attempted to breed during the preceding breeding season were measured. Birds were weighed using a 1000-g Pesola scale (Baar, Zug, Switzerland) and moult status was determined from plumage examination (de Beer et al., 2001). Birds were housed in individual shade cloth cages (0.15 m^3) in a room kept at outdoor ambient air temperature (5.0°C ± 1.8 SD, measured by a standard mercury thermometer). Water was provided *ad libitum*, but food was withheld until after metabolic measurements to ensure post-absorptive conditions. All birds were released within 26 hours of capture. The work was done under ethics permit 11NP_CHO01 from Stellenbosch University and with the approval of the Prince Edward Islands Management Committee.

Gas exchange measurements

Metabolic rate was estimated from measurements of oxygen consumption ($\dot{V}O_2$) obtained using an open flow-through respirometry system as set out in Lighton (2008) and set up at the island's research station. Birds were placed in a darkened 30L plastic chamber within a custom-built insulated environmental chamber. Air temperature within the environmental chamber was measured using two calibrated Thermocron iButton data loggers (Model DS1923, Dallas, Texas, USA).

Air was drawn from an unoccupied room using an air pump (Microvood, Italy) and passed through Bev-A-Line tubing (Thermoplastic Processes Inc., Georgetown, Delaware, USA) to a silica gel⁄ soda lime⁄ silica gel column which removed carbon dioxide and water vapour. Air flow was divided into two lines each regulated by a mass flow controller (Model 840, Sierra Instruments, Netherlands and MFC2, Sable Systems, Henderson, Nevada, USA). One line supplied the respirometry chamber at 8000 ml min^{-1}, ensuring adequate mixing in the chamber. The excurrent air from the chamber was subsampled with a subsampler mass flow meter unit (SS4; Sable Systems), passed through a soda lime⁄ silica gel column, and then to an Oxzilla II oxygen analyzer (Sable Systems) to measure fractional O_2 concentration. The second air line flowed directly to the oxygen analyzer to establish a base line and account for any temperature drift that may have occurred. Output from the oxygen analyzer was

digitized using a Universal Interface II (Sable Systems) and recorded on a personal computer using Expedata data acquisition software (Sable Systems), with a sampling interval of 1 s. Baseline O_2 from the cuvette was obtained for 20 min before and after each measurement.

The lowest 10 min mean $\dot{V}O_2$ over the test period was considered resting values, following Liknes et al. (2002). Because carbon dioxide and water vapour were scrubbed before and after entering the oxygen analyzer, oxygen consumption was calculated following Lighton (2008; equation 9.12). All measurements were obtained during the rest phase of the bird's circadian cycle. Measurements began no sooner than 30 minutes after sunset and ended no later than 30 minutes prior to sunrise. Individual measurement periods lasted three to six hours. To ensure birds were awake and resting calmly during measurements they were monitored inside the chamber with an infrared webcam (Genius eface 1325r, Taiwan). Time elapsed since capture was ≥9 h and birds could reasonably be considered to be postabsorptive. The oxygen analyzer was tested for temperature drift every 30 min.

The first five individuals were subjected to a ramped T_a profile during each test to determine the thermoneutral zone (TNZ). Each bird experienced three hours at temperatures between 1° C and 15° C during a single measurement session. Sheathbills alter their behaviour when experiencing exceptionally high temperatures (G.T.W. McClelland pers. obs.) and stressing the animals was a concern. We therefore chose 15° C as our maximum with the knowledge that it is almost double Marion Island's highest mean monthly temperature (le Roux, 2008), and higher than the daily maximum ambient temperature recorded on all but 2 % of days in the year (South African Weather Service, unpublished).

Statistical analyses

Oxygen consumption rate was corrected to ml O_2 h^{-1} at standard temperature and pressure, dry. Sheathbills were assumed to have an RQ of 0.79 and each individual's rate of oxygen consumption was converted to watts using a conversion factor of 20.1 kJ l^{-1} O_2 (Schmidt-Nielsen, 1997). Metabolic data were analyzed using analysis of covariance (ANCOVA) with body mass (M_b) as a covariate to control for the effect of body size on BMR (Watts). Tukey's HSD test was used in *post-hoc* comparisons. Least-squares linear regression models were fitted to metabolic rate and T_a data for estimates of TNZ. Analyses were performed in the

statistical software R 2.15.0 (R Development Core Team, 2010) and Statistica v.10 (StatSoft Inc., Tulsa, OK, USA).

Comparative analyses

To compare the BMR of sheathbills to those of other birds, phylogenetic signal in M_b and BMR was first tested for using randomization tests for the mean-squared error and by calculating the K-statistic (Blomberg et al., 2003, MatLab program PHYSIG_LL.m). Sheathbill BMR was then compared with those of birds in general using wild-caught populations of 135 species from McKechnie et al. (2006) which employed a phylogeny based primarily on Sibley and Alquist (1990). The comparison was then narrowed to other avian island endemics using 31 species from the literature (Table 1). Considering the paucity of measurements on island birds, data were included irrespective of sample size or population origin (wild-caught or captive raised) despite possible influences on results (McKechnie and Wolf, 2004; McKechnie et al., 2006). We did not include birds restricted to the island of New Guinea considering its recent (< 17 000 yr) separation from Australia (Voris, 2000). A phylogeny was constructed based on that of Hackett et al. (2008), with relationships within the Psittaciformes, Columbiformes, Gruiformes, Anseriformes, and Apterygiformes based on Wright et al. (2008), Gibb and Penny (2010), Livezey (1998), Donne-Gousse et al. (2002), and Baker et al. (1995), respectively. Since all the branch lengths in the phylogeny were not known, all branches in the model were set as equal. The phylogenetic variance–covariance matrix required for these analyses was obtained using the PDAP suite (Garland and Ives, 2000) within the program Mesquite (Maddison and Maddison, 2011) from the respective phylogenies. Since M_b ($K = 0.698$, $P < 0.001$) and BMR ($K = 0.553$, $P < 0.001$) both exhibited significant phylogenetic signals, phylogenetically independent prediction intervals based on the sheathbill's position within the phylogeny were calculated (Garland and Ives, 2000).

Results

The lowest metabolic rates in the ramped T_a profile were recorded at 15°. This falls within the range of thermoneutral zones observed in other high latitude Charadriiformes (Kendeigh et al., 1977; Gabrielsen et al., 1988, 1991; Bryant and Furness, 1995) and we assume birds were in their TNZ.

Mean mass of the 22 sheathbills was 459.0 g (SD = 64, min = 360, max = 600). Mean whole-animal BMR was 2.370 W (SD = 0.464, min = 1.599, max = 3.165) and mass-specific BMR was 5.145 mW g^{-1} (SD = 0.715, min = 4.099, max = 6.513).

The slopes of the phylogenetic generalized least squares (PGLS) regressions were logBMR = -1.434 + 0.656 $logM_b$ (GLM: $F_{(1, 139)}$ = 1063.4, $p > 0.001$, r^2 = 0.887) for all wild-caught populations, and -1.366 logBMR + 0.619 $logM_b$ (GLM: $F_{(1, 30)}$ = 254.9, $p > 0.001$, r^2 = 0.895) for island birds. The BMR datum for sheathbills fell within the 95% confidence and 95% prediction intervals when compared to both other wild-caught populations (Fig. 3), and birds restricted to islands (Fig. 4).

Body mass and basal metabolic rate differed significantly between the two sheathbill populations (Table 2, Fig. 5). Mean KP sheathbill body mass was 20.4 % greater than that of RH sheathbills (Student's t-test: t = 4.22, d.f. = 20, $p < 0.001$). Mass-corrected BMR differed significantly by habitat type (GLM: $F_{(2, 19)}$ = 18.01, $p < 0.001$, r^2 = 0.655), but not sex or moult score. Least-squares means revealed that BMR in KP sheathbills was 25.0 % higher than that of RH sheathbills ($F_{(1, 19)}$ = 9.835, p = 0.006).

Discussion

Black-faced sheathbills are both phylogenetically and ecologically distinct from many other avian taxa given their position within the Charadriiformes and status as one of the few high latitude island endemics. In consequence, it was predicted that, as is the case for other ecologically distinct island endemics, metabolic rates in this species might be unusual by comparison with other birds. By contrast, the present data suggest that the BMR of sheathbills is typical for a bird of its size. Sheathbills fell within the 95% prediction intervals of the PGLS regression for both wild-caught birds and island-restricted species. Though the prediction intervals in both analyses were relatively wide, partially a reflection of the distant relationship between sheathbills and other species in the respective phylogenies (Garland and Ives, 2000), the relatively close proximity of sheathbills to the PGLS regression line suggests narrower intervals would do little to alter this conclusion. However, one limitation of comparing wild-caught sheathbills to the other species in the island bird phylogeny is the predominance of captive-raised birds in the dataset, which scale to a different exponent of that of wild-caught birds (McKechnie et al., 2006; White, Blackburn, et al., 2007). Thus, the

observation that sheathbills fail to differ from other island species should be tempered by the fact that it might be subject to change when data are available incorporating measurements from a greater number of wild-caught populations of other bird species.

Mass-corrected BMR was found to vary by up to 37.1% between individual sheathbills and to differ significantly between the two groups. A possible driver of this variation is habitat quality and its associated behaviours. Polychaete worms have lower energetic values than most benthic invertebrates (Griffiths, 1977) and provide considerably less energy than the food items consumed most frequently in penguin colonies (Table 3). In addition, the accessibility of the intertidal zone is contingent on tides and sea surface conditions, which interfere with foraging 25.6 % of days (McClelland and Chown unpublished data). During the winter months RH sheathbills therefore likely forage on a diet that is of less quality and predictability than KP sheathbills. Thus, sheathbills occupying a superior habitat had higher mass-corrected metabolic rates in comparison to sheathbills occupying a lower quality habitat despite all individuals experiencing identical environmental (temperature, rainfall, humidity, solar radiation, and wind) conditions.

Basal metabolic rate is often thought to be associated with habitat quality and several hypotheses have been proposed to account for the phenomenon including the food habits hypothesis (McNab, 1986), and the “bowtie effect” (Lovegrove, 2000). Both theories posit that species or populations that exploit a diet of high quality, availability, and/or predictability are likely to exhibit high mass-corrected BMRs while lower BMRs are more likely to occur when faced with a diet of low quality, availability and/or predictablity. Within-species investigations into the relationship between BMR and habitat quality are advantageous in that they avoid the potentially confounding effect of phylogeny found in interspecific analyses (Garland et al., 1999). However, while intraspecific analyses may offer greater precision when investigating sources of variation, confounding factors may still lead to uncertainty. Comparisons are often made between geographically separated populations within a species, where each population is almost certainly under its own selection pressure from its environment on a local scale (Holt and Gaines, 1992; Hoffman and Blows, 1994). For example, populations are often energetically different along latitudinal and elevational gradients (Wikelski et al., 2003; Broggi et al., 2005; Dunbar and Brigham, 2010; Maggini and Bairlein, 2013), possibly in response to the increased cost of maintaining body temperature

at colder ambient temperatures (Calder and King, 1974; Daan et al., 1990; Jankowski et al., 2013). Separating the effects of habitat quality from environment and local adaptation in these studies can therefore be difficult, inviting ambiguity into proximate causes. The two sympatric yet distinct groups of sheathbills on Marion Island overcome this problem and represent a natural common-garden experiment, albeit a limited one as two population comparisons are inherently limited (Garland and Adolph, 1994). It should also be noted that other factors may be working to shape sheathbill BMR. For example, territorial behaviour differs between the two groups (Burger, 1982, 1984) and this may play a role. Nevertheless, the current data suggest that when free of the effects of environmental conditions, there is a clear positive correlation between habitat quality and BMR in free-living birds.

Conclusion

Sheathbills are the only terrestrial endemic birds present on Marion Island and the only terrestrial bird species present on all four Southern Ocean archipelagos. The intraspecific variation in BMR recorded in this study may play an important role in the species' ability to persist where others have not. Island birds often undergo a niche expansion, demonstrated by an increased range of morphologies and foraging behaviours when compared to their mainland progenitors (Van Valen, 1965; Blondel, 2000; Whittaker and Fernández-Palacios, 2007). Niche expansion reduces the number of conspecifics that a given individual will compete with (Roughgarden, 1972; Dayan and Simberloff, 2005; Svanbäck and Bolnick, 2007) and allows a species to maximize its population size (Van Valen, 1965). In turn, greater population size helps insure persistence against demographic and environmental stochasticity (Shaffer, 1981, 1987; Lande, 1993). This insular shift may not reflect a trend towards a population of generalists, but rather be the product of high intraspecific variation from individual specialists (Werner and Sherry, 1987; Scott et al., 2003; Myers et al., 2010). There is no reason to assume that this broadening of traits does not extent to physiology. Indeed, the fitness consequences of a given metabolic rate have been demonstrated to be context-specific (Steyermark et al., 2005; Reid et al., 2012) and high variation may allow species to maximize fitness over the widest possible range of environmental gradients (Burton et al., 2011). Unfortunately at present too few studies have examined intraspecific variation within island species to address the hypothesis. For example, a search of the literature found only one other endemic bird species (Puerto Rican tody, *Todus mexicanus* Lesson; Merola-Zwartjes and Ligon, 2000) that has been studied to a

degree that would allow meaningful intraspecific analysis (wild-caught, n > 10). The high variation observed in sheathbills suggests greater focus on the energetic of endemic birds may reveal additional adaptations to island living.

References

Araújo, M.S., Bolnick, D.I., Layman, C.A., 2011. The ecological causes of individual specialisation. Ecology Letters 14, 948–958.

Baker, A.J., Daugherty, C.H., Colbourne, R., McLennan, J.L., 1995. Flightless brown kiwis of New Zealand possess extremely subdivided population structure and cryptic species like small mammals. Proceedings of the National Academy of Sciences of the U.S.A. 92, 8254–8258.

De Beer, S.J., Lockwood, G.M., Raijmakers, J.H.F.A., Raijmakers, J.M.H., Scott, W.A., Oschadleus, H.D., Underhill, L.G., 2001. SAFRING Bird Ringing Manual. ADU Guide 5, Management Services. Avian Demography Unit, University of Cape Town, Cape Town.

Bininda-Edmonds, O.R.P., 2004. Phylogenetic supertrees: combining information to reveal the tree of life. Kluwer Academic Publishers, Dordrecht.

Bininda-Edmonds, O.R.P., Gittleman, J.L., 2000. Are pinnipeds functionally different from fissiped carnivores? The importance of phylogenetic comparative analyses. Evolution 54, 1011–1023.

Biro, P.A., Stamps, J.A., 2010. Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? Trends in Ecology and Evolution 25, 653–659.

Blomberg, S.P., Garland, T., Ives, A.R., 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. Evolution 57, 717–745.

Blondel, J., 2000. Evolution and ecology of birds on islands: trends and prospects. Vie Et Milieu 50, 205–220.

Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., Rudolf, V.H.W., Schreiber, S.J., Urban, M.C., Vasseur, D.A., 2011. Why intraspecific trait variation matters in community ecology. Trends in Ecology and Evolution 26, 183–192.

Bozinovic, F., Ruiz, G., Rosenmann, M., 2004. Energetics and torpor of a South American "living fossil", the microbiotheriid *Dromiciops gliroides*. Journal of Comparative Physiology B 174, 293–297.

Broggi, J., Hohtola, E., Orell, M., Nilsson, J.-A., 2005. Local adaptation to winter conditions in a passerine spreading north: a common-garden approach. Evolution 59, 1600–1603.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. Ecology 85, 1771–1789.

Bryant, D.M., 1997. Energy expenditure in wild birds. Proceedings of the Nutrition Society 56, 1025–1039.

Bryant, D.M., Furness, R.W., 1995. Basal metabolic rates of North Atlantic seabirds. Ibis 137, 219–226.

Burger, A.E., 1981. Time budgets, energy needs, and kleptoparasitism in breeding lesser sheathbills (*Chionis minor*). Condor 83, 106–112.

Burger, A.E., 1982. Foraging behaviour of lesser sheathbills *Chionis minor* exploiting invertebrates on a Sub-Antarctic island. Oecologia 52, 236–245.

Burger, A.E., 1984. Winter territoriality in lesser sheathbills on breeding grounds at Marion Island. Wilson Journal of Ornithology 96, 20–33.

Burton, T., Killen, S.S., Armstrong, J.D., Metcalfe, N.B., 2011. What causes intraspecific variation in resting metabolic rate and what are its ecological consequences? Proceedings of the Royal Society B 278, 3465–3473.

Calder, W.A., King, J.R., 1974. Thermal and caloric relations of birds, in: Farner, D.S., King, J.R. (Eds.), Avian Biology Volume IV. Academic Press, New York, pp. 259–413.

Chown, S.L., Froneman, P.W., 2008. The Prince Edward Islands: land-sea interactions in a changing ecosystem. Sun Press, Stellenbosch.

Chown, S.L., Gaston, K.J., Kleunen, M., Clusella-Trullas, S., 2010. Population responses within a landscape matrix: a macrophysiological approach to understanding climate change impacts. Evolutionary Ecology 24, 601–616.

Clarke, A., Rothery, P., Isaac, N.J.B., 2010. Scaling of basal metabolic rate with body mass and temperature in mammals. The Journal of Animal Ecology 79, 610–619.

Daan, S., Masman, D., Groenewold, A., 1990. Avian basal metabolic rates: their association with body composition and energy expenditure in nature. American Journal of Physiology 259, 333–340.

Dayan, T., Simberloff, D., 2005. Ecological and community-wide character displacement: the next generation. Ecology Letters 8, 875–894.

Donne-Gousse, C., Laudet, V., Hanni, C., 2002. A molecular phylogeny of anseriformes based on mitochondrial DNA analysis. Molecular Phylogenetics and Evolution 23, 339–356.

Dunbar, M.B., Brigham, R.M., 2010. Thermoregulatory variation among populations of bats along a latitudinal gradient. Journal of Comparative Physiology B 180, 885–893.

Gabrielsen, G.W., Mehlum, F., Karlsen, H.E., 1988. Thermoregulation in four species of arctic seabirds. Journal of Comparative Physiology B 157, 703–708.

Gabrielsen, G.W., Taylor, J.R.E., Konarzewski, M., Mehlum, F., 1991. Field and laboratory metabolism and thermoregulation in dovekies (*Alle alle*). Auk 108, 71–78.

Garland, T., Adolph, S.C., 1994. Why not to do two-species comparative studies: limitations on inferring adaptation. Physiological Zoology 67, 797–828.

Garland, T., Midford, P.E., Ives, A.R., 1999. An introduction to phylogenetically based statistical methods, with a new method for confidence intervals on ancestral values. American Zoologist 39, 374–388.

Garland, T.J., Ives, A.R., 2000. Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. American Naturalist 155, 346–364.

Gibb, G.C., Penny, D., 2010. Two aspects along the continuum of pigeon evolution: a South-Pacific radiation and the relationship of pigeons within Neoaves. Molecular Phylogenetics and Evolution 56, 698–706.

Gotelli, N.J., Anderson, M.J., Arita, H.T., Chao, A., Colwell, R.K., Connolly, S.R., Currie, D.J., Dunn, R.R., Graves, G.R., Green, J.L., Grytnes, J.-A., Jiang, Y.-H., Jetz, W., Kathleen Lyons, S., McCain, C.M., Magurran, A.E., Rahbek, C., Rangel, T.F.L.V.B., Soberón, J., Webb, C.O., Willig, M.R., 2009. Patterns and causes of species richness: a general simulation model for macroecology. Ecology Letters 12, 873–886.

Griffiths, D., 1977. Caloric variation in Crustacea and other animals. The Journal of Animal Ecology 46, 593–605.

Hackett, S.J., Kimball, R.T., Reddy, S., Bowie, R.C.K., Braun, E.L., Braun, M.J., Chojnowski, J.L., Cox, W.A., Han, K.-L., Harshman, J., Huddleston, C.J., Marks, B.D., Miglia, K.J., Moore, W.S., Sheldon, F.H., Steadman, D.W., Witt, C.C., Yuri, T., 2008. A phylogenomic study of birds reveals their evolutionary history. Science 320, 1763–1768.

Hayssen, V., Lacy, R.C., 1985. Basal metabolic rate in mammals: taxonomic differences in the allometry of BMR and body mass. Comparative Biochemistry and Physiology 8, 741–754.

Hoffman, A.A., Blows, M.W., 1994. Species borders: ecological and evolutionary perspectives. Trends in Ecology and Evolution 9, 223–227.

Holt, R.D., Gaines, M.S., 1992. Analysis of adaptation in heterogeneous landscapes: implications for the evolution of fundamental niches. Evolutionary Ecology 6, 433–447.

Huyser, O., Ryan, P.G., Cooper, J., 2000. Changes in population size, habitat use and breeding biology of lesser sheathbills (*Chionis minor*) at Marion Island: impacts of cats, mice and climate change? Biological Conservation 92, 299–310.

Jankowski, J.E., Londoño, G.A., Robinson, S.K., Chappell, M.A., 2013. Exploring the role of physiology and biotic interactions in determining elevational ranges of tropical animals. Ecography 36, 1–12.

Jetz, W., Freckleton, R.P., McKechnie, A.E., 2008. Environment, migratory tendency, phylogeny and basal metabolic rate in birds. PloS one 3, e3261.

Jung, V., Violle, C., Mondy, C., Hoffmann, L., Muller, S., 2010. Intraspecific variability and trait-based community assembly. Journal of Ecology 98, 1134–1140.

Kendeigh, S.C., Dolnik, V.R., Gavrilov, V.M., 1977. Avian energetics, in: Pinowski, J., Kendeigh, S.C. (Eds.), Granivorous Birds in Ecosystems. Cambridge University Press, New York, pp. 127–204.

Konarzewski, M., Książek, A., 2012. Determinants of intra-specific variation in basal metabolic rate. Journal of Comparative Physiology B 183, 27–41.

Kozlowski, J., Konarzewski, M., 2004. Is West , Brown and Enquist's model of allometric scaling mathematically correct and biologically relevant? Functional Ecology 18, 283–289.

Kraft, N.J.B., Cornwell, W.K., Webb, C.O., Ackerly, D.D., 2007. Trait evolution, community assembly, and the phylogenetic structure of ecological communities. American Naturalist 170, 271–283.

Krogh, A., 1914. The quantitative relation between temperature and standard metabolism in animals. Internationale Zeitschrift für Physikalisch-Chemische Biologie 1, 491–508.

Lande, R., 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist 142, 911–927.

Lighton, J.R.B., 2008. Measuring metabolic rates: a manual for scientists, 1st ed. Oxford University Press.

Liknes, E.T., Scott, S.M., Swanson, D.L., 2002. Seasonal acclimatization in the American goldfinch revisited: to what extent do metabolic rates vary seasonally? Condor 104, 548–557.

Livezey, B.C., 1998. A phylogenetic analysis of the Gruiformes (Aves) based on morphological characters, with an emphasis on the rails (Rallidae). Philisophical Transactions of the Royal Society B 353, 2077–2151.

Livezey, B.C., 2010. Phylogenetics of modern shorebirds (Charadriiformes) based on phenotypic evidence: analysis and discussion. Zoological Journal of the Linnean Society 160, 567–618.

Lovegrove, B.G., 2000. The zoogeography of mammalian basal metabolic rate. American Naturalist 156, 201–219.

Lovegrove, B.G., Perrin, M.R., Brown, M., 2011. The allometry of parrot BMR: seasonal data for the greater vasa parrot, *Coracopsis vasa*, from Madagascar. Journal of Comparative Physiology B 181, 1075–1087.

Maddison, W.P., Maddison, D.R., 2011. Mesquite: a modular system for evolutionary analysis. version 2.74, 2010. URL http://mesquiteproject.org.

Madritch, M.D., Hunter, M.D., 2002. Phenotypic diversity influences ecosystem functioning in an oak sandhills community. Ecology 83, 2084–2090.

Maggini, I., Bairlein, F., 2013. Metabolic response to changes in temperature in northern wheatears from an arctic and a temperate populations. Journal of Avian Biology doi: 10.1111/j.1600–048X.2013.05869.x.

McKechnie, A.E., Freckleton, R.P., Jetz, W., 2006. Phenotypic plasticity in the scaling of avian basal metabolic rate. Proceedings of the Royal Society B 273, 931–937.

McKechnie, A.E., Wolf, B.O., 2004. The allometry of avian basal metabolic rate: good predictions need good data. Physiological and Biochemical Zoology 77, 502–521.

McNab, B.K., 1986. The influence of food habits on the energetics of eutherian mammals. Ecological Monographs 56, 1–19.

McNab, B.K., 1992. A statistical analysis of mammalian rates of metabolism. Functional Ecology 6, 672–679.

McNab, B.K., 1995. Energy expenditure and conservation in frugivorous and mixed-diet carnivorans. Journal of Mammalogy 76, 206–222.

McNab, B.K., 1996. Metabolism and temperature regulation of kiwis (Apterygidae). Auk 113, 687–692.

McNab, B.K., 2000. The influence of body mass, climate, and distribution on the energetics of South Pacific pigeons. Comparative Biochemistry and Physiology A 127, 309 – 329.

McNab, B.K., 2002. Minimizing energy expenditure facilitates vertebrate persistence on oceanic islands. Ecology Letters 5, 693–704.

McNab, B.K., 2003a. Ecology shapes bird energetics. Nature 426, 620–621.

McNab, B.K., 2003b. The energetics of New Zealand' s ducks. Comparative Biochemistry and Physiology, Part A 135, 229–247.

McNab, B.K., 2009. Ecological factors affect the level and scaling of avian BMR. Comparative Biochemistry and Physiology A 152, 22–45.

McNab, B.K., Ellis, H.I., 2006. Flightless rails endemic to islands have lower energy expenditures and clutch sizes than flighted rails on islands and continents. Comparative Biochemistry and Physiology A 145, 295–311.

McNab, B.K., Salisbury, C.A., 1995. Energetics of New Zealand's temperate parrots. New Zealand Journal of Zoology 22, 339–349.

Melian, C.J., Vilas, C., Baldo, F., González-Ortegon, E., Drake, P., Williams, R.J., 2011. Eco-evolutionary dynamics of individual-based food webs. Advances in Ecological Research 45, 225–268.

Merola-Zwartjes, M., Ligon, J.D., 2000. Ecological energetics of the Puerto Rican tody: heterothermy, torpor, and intra-island variation. Ecology 81, 990–1003.

Myers, S., Brown, G., Kleindorfer, S., 2010. Divergence in New Holland honeyeaters (*Phylidonyris novaehollandiae*): evidence from morphology and feeding behavior. Journal of Ornithology 151, 287–296.

Phillimore, A.B., Freckleton, R.P., Orme, C.D.L., Owens, I.P.F., 2006. Ecology predicts large-scale patterns of phylogenetic diversification in birds. American Naturalist 168, 220–229.

R Development Core Team, 2010. R: A language and environment for statistical computing. http://www.r-project.org.

Reid, D., Armstrong, J.D., Metcalfe, N.B., 2012. The performance advantage of a high resting metabolic rate in juvenile salmon is habitat dependent. Journal of Animal Ecology 81, 868–875.

Roughgarden, J., 1972. Evolution of niche width. American Naturalist 106, 683–718.

le Roux, P.C., 2008. Climate and climate change, in: Chown, S.L., Froneman, P.W. (Eds.), The Prince Edward Islands: Land-Sea Interactions in a Changing Ecosystem. Sun Press, Stellenbosch, pp. 39–64.

Ryan, P.G., Watkins, B.P., Siegfried, W.R., 1989. Morphometrics, metabolic rate and body temperature of the smallest flightless bird: the Inaccessible Island rail. Condor 91, 465–467.

Schleucher, E., Withers, P.C., 2002. Metabolic and thermal physiology of pigeons and doves. Physiological and Biochemical Zoology 75, 439–450.

Schmidt-Nielsen, K., 1997. Animal physiology: adaptation and environment, 5th ed. Cambridge University Press, Cambidge.

Scott, S.N., Clegg, S.M., Blomberg, S.P., Kikkawa, J., Owens, I.P.F., 2003. Morphological shift in island-dwelling birds: the roles of generalist foraging and niche expansion. Evolution 57, 2147–2156.

Shaffer, M.L., 1981. Minimum for species population sizes for species conservation. Bioscience 31, 131–134.

Shaffer, M.L., 1987. Minimum viable populations: coping with uncertainty, in: Soulé, M.E. (Ed.), Viable Populations for Conservation. Cambridge University Press, Cambridge, pp. 69–86.

Sibley, C.E., Alquist, J.E., 1990. Phylogeny and classification of birds. Yale University Press, New Haven.

Smith, V.R., 2002. Climate change in the sub-Antarctic: an illustration from Marion Island. Climatic Change 52, 345–357.

Speakman, J.R., 2000. The cost of living: field metabolic rates of small mammals. Advances in Ecological Research 30, 178–297.

Steimle, F.W., Terranova, R.J., 1985. Energy equivalents of marine organisms from the continental shelf of the temperate Northwest Atlantic. Journal of the Northwest Atlantic Fisheries Science 6, 117–124.

Steyermark, A.C., Miamen, A.G., Feghahati, H.S., Lewno, A.W., 2005. Physiological and morphological correlates of among-individual variation in standard metabolic rate in the leopard frog *Rana pipiens*. The Journal of Experimental Biology 208, 1201–1208.

Svanbäck, R., Bolnick, D.I., 2007. Intraspecific competition drives increased resource use diversity within a natural population. Proceedings of the Royal Society B 274, 839–844.

Tieleman, B.I., Versteegh, M.A., Helm, B., Dingemanse, N.J., 2009. Quantitative genetics parameters show partial independent evolutionary potential for body mass and metabolism in stonechats from different populations. Journal of Zoology 279, 129–136.

Van Valen, L.M., 1965. Morphological variation and width of ecological niche. American Naturalist 99, 377–390.

Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., Jung, V., Messier, J., 2012. The return of the variance: intraspecific variability in community ecology. Trends in Ecology and Evolution 27, 244–252.

Voris, H.K., 2000. Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. Journal of Biogeography 27, 1153–1167.

Weathers, W.W., 1979. Climatic adaptation in avian standard metabolic rate. Oecologia 89, 81–89.

Weathers, W.W., Riper III, C. Van, 1982. Temperature regulation in two endangered Hawaiian honeycreepers: the palila (*Psittirostra bailleui*) and the Laysan finch (*Psittirostra cantans*). Auk 99, 667–674.

Weathers, W.W., Weathers, D.L., Riper III, C. Van, 1983. Basal metabolism of the apapane: comparison of freshly caught birds with long-term captives. Auk 100, 977–978.

Webb, C.T., Hoeting, J.A., Ames, G.M., Pyne, M.I., LeRoy Poff, N., 2010. A structured and dynamic framework to advance traits-based theory and prediction in ecology. Ecology Letters 13, 267–283.

Weiher, E., Keddy, P.A., 1995. Assembly rules, null models, and trait dispersion: new questions from old patterns. Oikos 74, 159–164.

Werner, T.K., Sherry, T.W., 1987. Behavioral feeding specialization in *Pinaroloxias inornata*, the "Darwin's finch" of Cocos Island, Costa Rica. Proceedings of the National Academy of Sciences of the U.S.A. 84, 5506–5510.

White, C.R., Alton, L.A., Frappell, P.B., 2011. Metabolic cold adaptation in fishes occurs at the level of whole animal, mitochondria and enzyme. Proceedings of the Royal Society B 279, 1740–1747.

White, C.R., Blackburn, T.M., Martin, G.R., Butler, P.J., 2007. Basal metabolic rate of birds is associated with habitat temperature and precipitation, not primary productivity. Proceedings of the Royal Society B 274, 287–293.

White, C.R., Cassey, P., Blackburn, T.M., 2007. Allometric exponents do not support a universal metabolic allometry. Ecology 88, 315–323.

White, C.R., Frappell, P.B., Chown, S.L., 2012. An information-theoretic approach to evaluating the size and temperature dependence of metabolic rate. Proceedings of the Royal Society B 279, 3616–3621.

White, C.R., Kearney, M.R., 2012. Determinants of inter-specific variation in basal metabolic rate. Journal of Comparative Physiology B 183, 1–26.

Whittaker, R.J., Fernández-Palacios, J.M., 2007. Island biogeography. Ecology, evolution and conservation. Oxford University Press, Oxford, UK.

Wiersma, P., Muñoz-Garcia, A., Walker, A., Williams, J.B., 2007. Tropical birds have a slow pace of life. Proceedings of the National Academy of Sciences of the U.S.A. 104, 9340–9345.

Wikelski, M., Spinney, L., Schelsky, W., Scheuerlein, A., Gwinner, E., 2003. Slow pace of life in tropical sedentary birds: a common-garden experiment on four stonechat populations from different latitudes. Proceedings of the Royal Society B 270, 2383–2388.

Wright, T.F., Schirtzinger, E.E., Matsumoto, T., Eberhard, J.R., Graves, R., Sanchez, J.J., Capelli, S., Mu, H., Scharpegge, J., Chambers, K., Fleischer, R.C., 2008. A multilocus molecular phylogeny of the parrots (Psittaciformes): support for a Gondwanan origin during the Cretaceous. Molecular Biology and Evolution 25, 2141–2156.

Tables

Table 1: Avian species restricted to islands in which mass-specific basal metabolic rate have been investigated. For each species body mass (M_b), BMR (W/S), climate (Te = temperate, Tr = tropical), island size (L = > 100 000 km^2, I = >1 000 km^2, S = < 1 000 km^2), a volant (Y) or flightless (N) condition, origin (C = captive-raised, W = wild caught), and sample sizes are provided.

Species	M_b(g)	W/S	Climate	Island Size	Flight	Origin	*n*	Reference
Palila (*Loxioides bailleui*)	34.8	0.447	Tr	I	Y	C	4	1
‘Apapane (*Himatione sanguinea*)	13.5	0.300	Tr	I	Y	W/C	4/4	2
Tui (*Prosthemadera novaeseelandiae*)	144.2	1.106	Te	L	Y	C	Unknown	3
Kea (*Nestor notabilis*)	836.9	4.439	Te	L	Y	C	2	4
Kākā (*Nestor meridionalis*)	369.3	2.142	Te	L	Y	C	2	4
Greater Vasa Parrot (*Coracopsis vasa*)	454.0	4.372	Tr	L	Y	C	8	5
Yellow-crowned Parakeet (*Cyanoramphus auriceps*)	52.9	0.492	Te	L	Y	C	7	4
Red-crowned Parakeet (*Cyanoramphus novaezelandiae*)	56.1	0.622	Te	L	Y	C	8	4
Antipodes Parakeet (*Cyanoramphus unicolor*)	129.4	1.081	Te	S	Y	C	2	4
Puerto Rican Tody (*Todus mexicanus*)	6.3	0.114	Tr	I	Y	W	26	6
Black-faced Sheathbill (*Chionis minor*)	457.0	2.534	Te	S	Y	W	22	7
Takahē (*Porphyrio hochstetteri*)	2758.3	6.886	Te	L	N	C	2	8
Inaccessible Island Rail (*Atlantisia rogersi*)	39.4	0.225	Te	S	N	W	6	9
Weka (*Gallirallus australis*)	813.5	1.828	Te	L	N	C	1	8
Guam Rail (*Gallirallus owstoni*)	198.8	0.917	Tr	S	N	C	2	8
Metallic Pigeon (*Columba vitiensis*)	467.9	1.444	Tr	I	Y	C	2	10
White-crowned Pigeon (*Patagioenas leucocephala*)	251.9	1.344	Tr	I	Y	C	Unknown	10
Nicobar Pigeon (*Caloenas nicobarica*)	613.0	1.814	Tr	S	Y	C	3	10
Western Crowned Pigeon (*Goura cristata*)	2313.4	4.267	Tr	L	Y	C	6	10
Pacific Imperial Pigeon (*Ducula pacifica*)	333.4	0.794	Tr	S	Y	C	4	10
Island Imperial Pigeon (*Ducula pistrinaria*)	394.2	1.072	Tr	I	Y	C	3	10
New Zealand Pigeon (*Hemiphaga novaeseelandiae*)	435.6	1.883	Te	L	Y	C	3	10
Cloven-feathered Dove (*Drepanoptila holosericea*)	198.0	0.825	Tr	I	Y	C	2	11

Blue duck (*Hymenolaimus malacorhynchos*)	717.1	3.142	Te	L	Y	C	3	12
Paradise Shelduck (*Tadorna variegata*)	1193.6	3.344	Te	L	Y	C	2	12
Black teal (*Aythya novaeseelandiae*)	488.4	2.333	Te	L	Y	C	2	12
Auckland Teal (*Anas aucklandica*)	373.1	1.875	Te	S	N	C	2	12
Brown Teal (*Anas chlorotis*)	528.8	2.319	Te	L	Y	C	2	12
Campbell Island Teal (*Anas nesiotis*)	371.1	1.650	Te	S	N	C	2	12
Southern Brown Kiwi (*Apteryx australis*)	3137.0	4.611	Te	L	N	C	3	13
Great Spotted Kiwi (*Apteryx haastii*)	2529.0	5.283	Te	L	N	C	2	13
Little Spotted Kiwi (*Apteryx owenii*)	1377.0	3.947	Te	L	N	C	2	13

References: 1. Weathers and Riper III (1982), 2. Weathers et al. (1983), 3. McNab (2009), 4. McNab and Salisbury (1995), 5. Lovegrove et al. (2011), 6. Merola-Zwartjes and Ligon (2000), 7. This study, 8. McNab and Ellis (2006), 9. Ryan et al. (1989), 10. McNab (2000), 11. Schleucher and Withers (2002), 12. McNab (2003), 13. McNab (1996).

Table 2: Differences in mean body mass (g, ± SD), whole-animal basal metabolic rate (WA BMR), and mass-specific basal metabolic rate (MS BMR) in black-faced sheathbills breeding in rockhopper (RH) and king penguin (KP) colonies on Marion Island.

Population	Body Mass (g)	WA BMR (W)	MS BMR (W)	*n*
RH Sheathbills	421.3 ± 44.2	2.047 ± 0.303	4.879 ± 0.690	10
KP Sheathbills	507.5 ± 51.7	2.758 ± 0.291	5.464 ± 0.635	12

Table 3: Energy value of the main food items consumed by black-faced sheathbills foraging in king penguin colonies and the intertidal zone on Marion Island.

Habitat	Food Item	kJ g^{-1} wet mass
King penguin colonies	Kleptoparasitism[1]	4.5 – 6.8
	Penguin carcasses[1]	4.9 – 11.6
	Penguin excreta[1]	2.1
Intertidal zone	Polychaete worms[2]	2.68 – 4.58

[1]Burger 1984
[2]Steimle and Terranova 1985 and references therein. Published mean values of species within Class Polychaeta.

Figure Legends

Figure 1: Sheathbill study area depicting the territory locations of measured KP (K) and RH (R) sheathbills, and the island research station (blocked "M").

Figure 2: Phylogeny of 32 avian species occurring on islands in which mass-specific basal metabolic rate have been investigated.

Figure 3: The PGLS allometry of the BMR of 137 wild-caught avian species with a least squares regression through the origin (black line). The grey dashed and dotted lines represent the 95% confidence and prediction intervals, respectively. The body mass and basal metabolic rate values for the black-faced sheathbill are highlighted in red. The regression equation was $\log BMR = -1.437 + 0.656 \log M_{b.}$

Figure 4: The PGLS allometry of the BMR of 32 avian species restricted to islands with a least squares regression through the origin (black line). The grey dashed and dotted lines represent the 95% confidence and prediction intervals, respectively. The black-faced sheathbill is highlighted in red. The regression equation was $-1.369 \log BMR + 0.617 \log M_{b.}$

Figure 5: Mean ± SD log-transformed BMR in sheathbills foraging in king (blue) and rockhopper penguin (red) colonies on Marion Island.

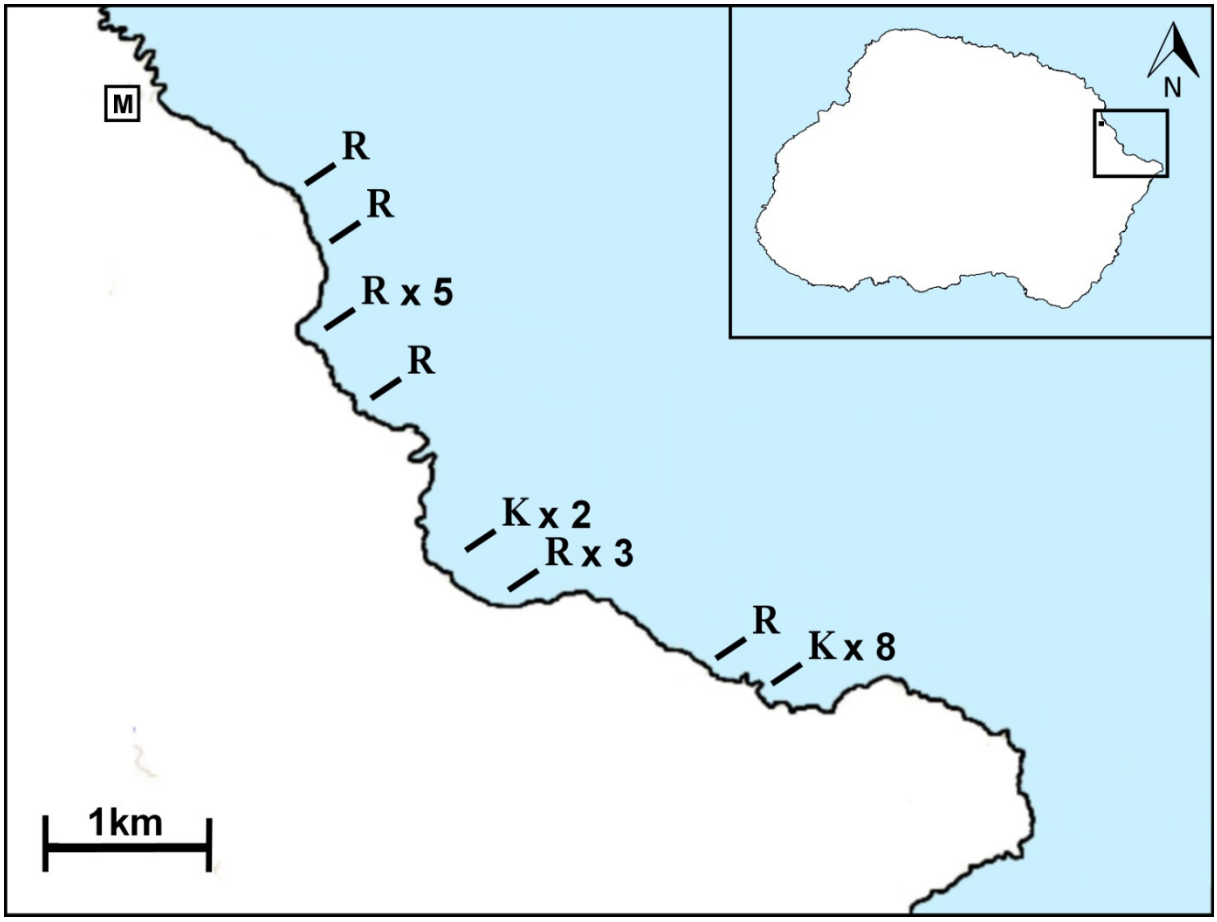


Figure 1

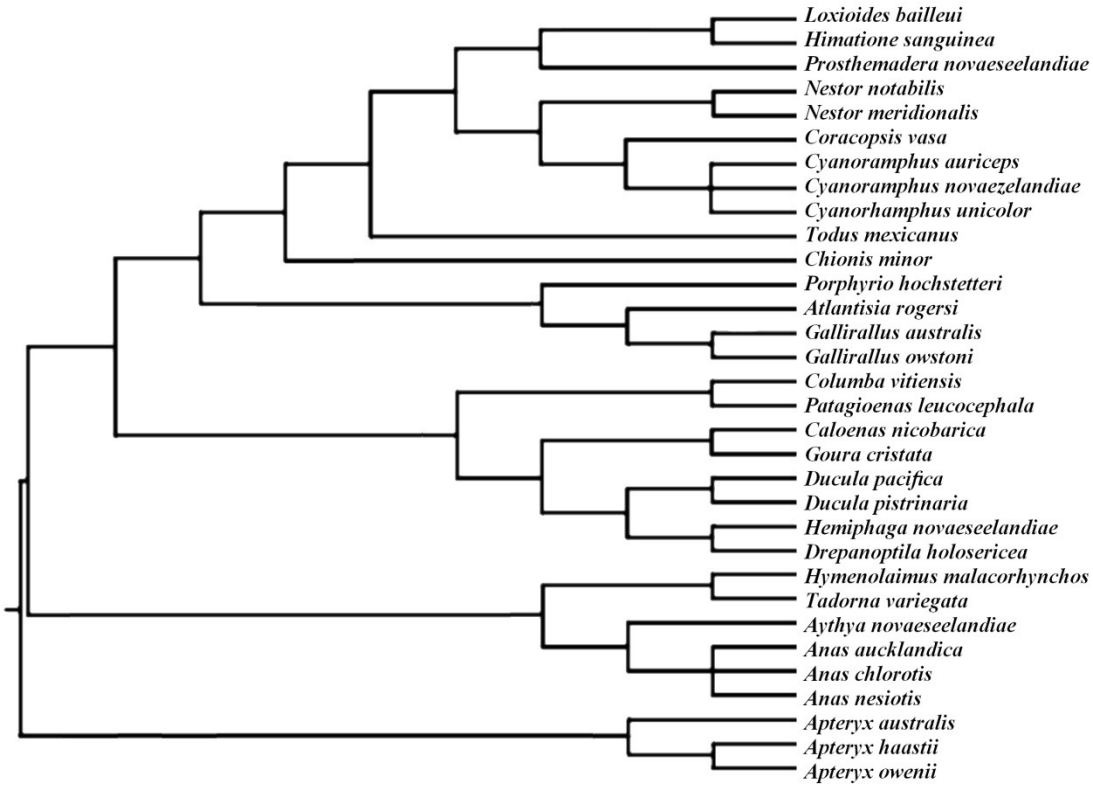


Figure 2

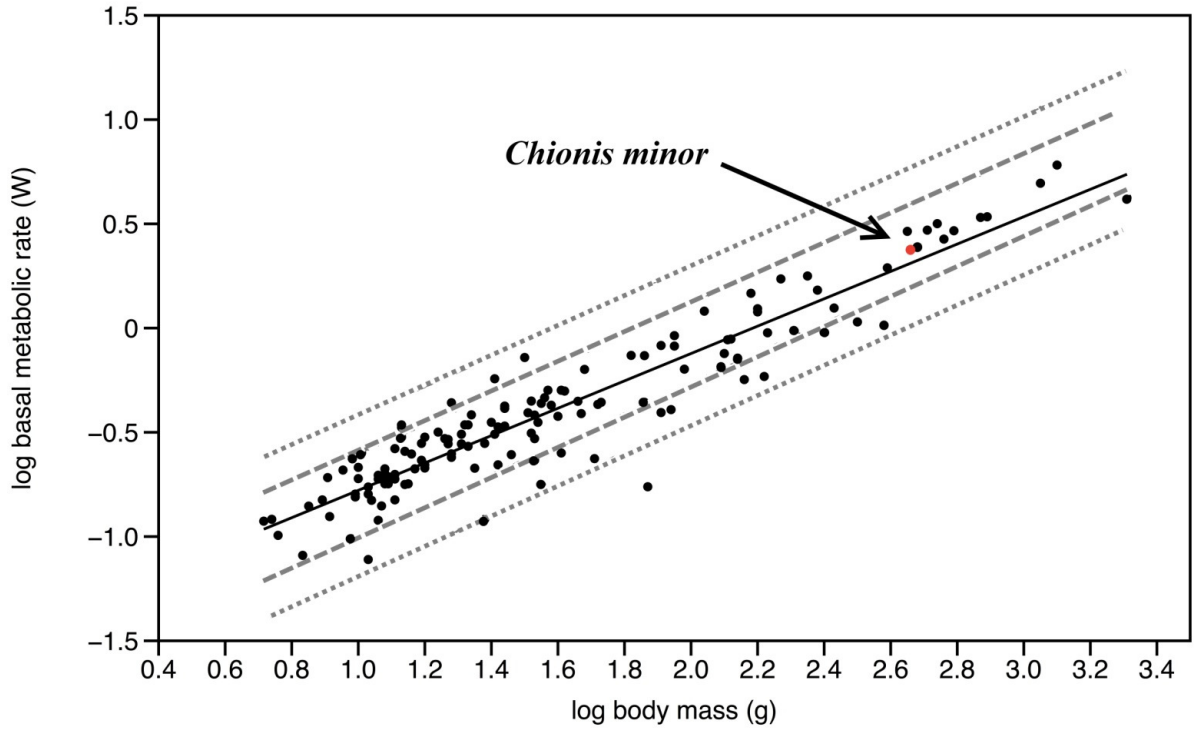


Figure 3

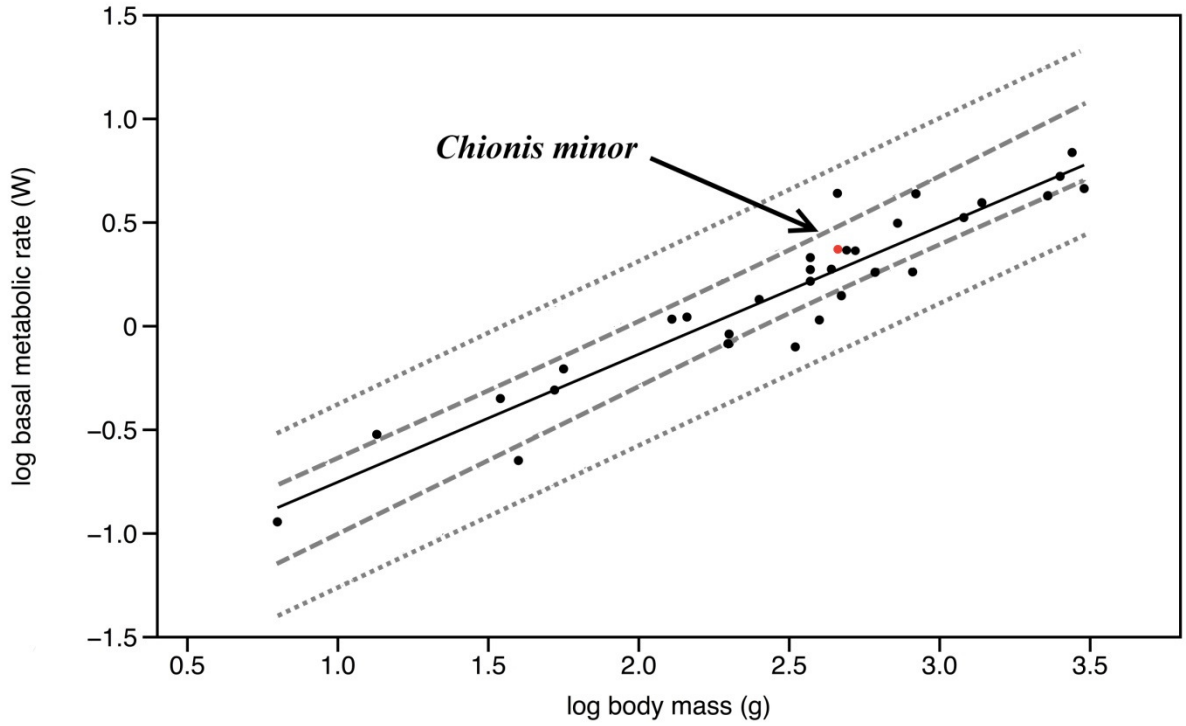


Figure 4

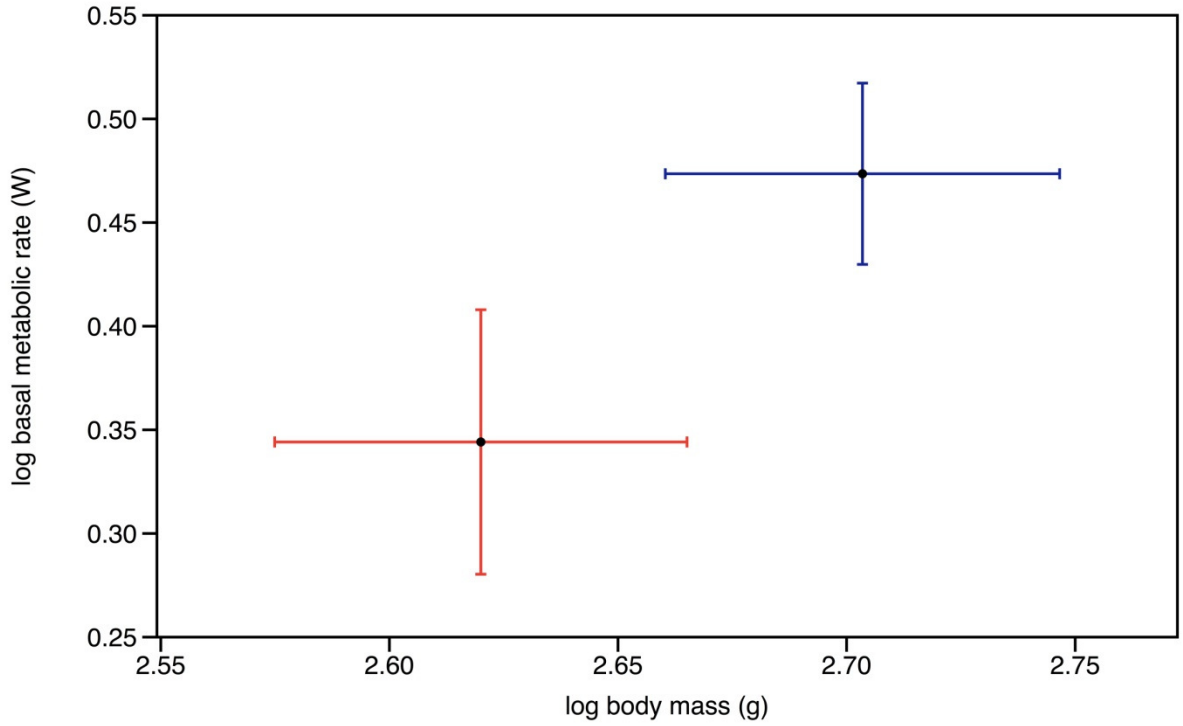


Figure 5

Chapter 5 – Conclusions

"He is most Haematopus-like in his motions, moving with great swiftness, and feeding on meat, which he holds down between his feet and tears into shreds. He is very fearless, and attacked the cats which came near him" **– E.L. Layard, Crozet Islands, 1867**

Black-faced sheathbill (*Chionis minor marionensis*), with macaroni penguin (*Eudyptes chrysolophus*) skull, Swartkops Point area, Marion Island

The combined effects of climate change and invasive species on the ecology of black-faced sheathbills (*Chionis minor*) on Marion Island

The interactive effects between global change drivers are being revealed with increasing frequency and there is growing evidence that these interactions may be almost as important as those of each driver alone (Didham et al., 2007; Mora et al., 2007; Brook et al., 2008; Crain et al., 2008). For invasive species and climate change, it has been suggested that warming temperatures will exacerbate the effects of many invasive species, so further impacting both diversity and ecosystem functioning (Dukes and Mooney, 1999; Chown and Convey, 2007; Walther et al., 2009). However, while support for such interactions is accumulating (Stachowicz et al., 2002; Chown et al., 2007; Willis et al., 2010), empirical examples of native species responses are limited (Brook et al., 2008; Walther et al., 2009; Sorte et al., 2013) and much uncertainty remains (Didham et al., 2007; Hellmann et al., 2008; Bellard et al., 2012). A contributing factor may be that just as the interactions between drivers of change can be complex, so too are the interactions of organisms within a community. These biotic networks can be highly responsive to environmental disturbance (Gilman et al., 2010; Bellard et al., 2012; Wisz et al., 2013), yet difficult to quantify (McCann, 2007). This thesis thus adopted an integrated approach to demonstrate empirically the subtle, but significant changes to an island endemic's demography and habitat use as a result of the combined effects of climate change and invasive species.

Synthesis

The results of this study demonstrate that the observed changes in black-faced sheathbill demography and habitat use on Marion Island are the consequence of the interactions between invasive house mice (*Mus musculus* Linnaeus) and climate change. The form of these interactions is represented graphically in Fig 1, with each of the links discussed in a synthetic context below. Most of these links were explicitly investigated as part of this thesis, or are based on a review of the extant published information (such as climate change).

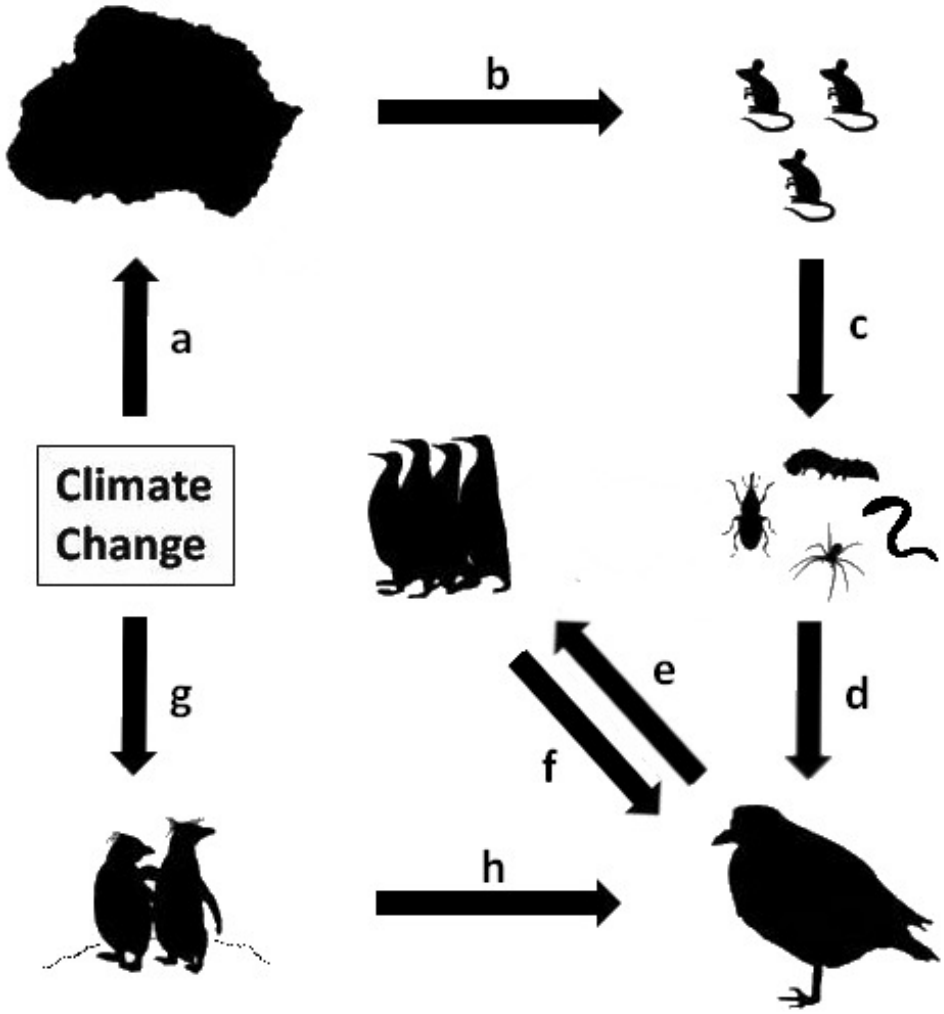


Figure 1: Flow chart of how climate change and invasive house mice on Marion Island interact to alter sheathbill ecology.

(a) Mean annual temperature has increased by more than 1° C and precipitation declined by more than 800 mm on Marion Island over the last half century as a result of the local effects of global climate change (Le Roux and McGeoch, 2008).

(b) In turn, the total number of mice on the island at peak density has increased by 145.6 % over the past decade, due largely to an extended breeding season and the amelioration of formally marginal habitats (Chapter 2).

(c) Mice continue to be primarily predators of terrestrial invertebrates. The subsequent increase in mouse predation pressure resulted in invertebrate biomass losses ranging between 82.8 % and 97.3 % in the two most important vegetation habitats for sheathbills, the biotic and mire habitats, respectively (Chapter 2).

(d) The significant reduction in invertebrate biomass effectively displaced sheathbills from a formerly important food resource, as confirmed by energetic analysis (Chapter 3) estimated from metabolic rate measurements (Chapter 4). As a result, the body condition of sheathbill females overwintering outside of king penguin colonies has declined significantly (Chapter 3).

(e) Further, up to 75.7 % of sheathbills that would traditionally forage for invertebrates in the winter have shifted into king penguin colonies (Chapter 3).

(f) The increased number of sheathbills foraging in king penguin colonies has meant a decrease in the number of penguins available per sheathbill by 39.6 %, leading to poorer female body condition amongst sheathbills breeding in these areas (Chapter 3).

(g) The number of rockhopper penguins on the island declined by up to 74 % between 1994-95 and 2008-09 (Crawford et al., 2009), part of a global decline largely attributed to climate change (Cunningham and Moors, 1994; Forcada and Trathan, 2009; Dehnhard et al., 2013).

(h) The majority of sheathbills on Marion Island are dependent on rockhopper penguins for breeding resources. Fewer breeding penguins equate to fewer egg predation and kleptoparasitism opportunities. A parallel decline in penguin food loads intended for offspring undoubtedly compounds the sheathbill resource shortage.

The sum of these changes to sheathbill ecology is fewer resources throughout the year, specifically for females, and sheathbills of both sexes have responded in several ways. However, the most notable outcome is a skew towards females in the tertiary sex ratio, a response to poor adult body condition. This bias towards the production of female offspring is forecast to increasingly manifest in the adult sex ratio. Population models suggest that sheathbills are currently suffering from density-dependent effects and that there are too few breeding territories because of rockhopper penguin declines. However, the number of males is projected to eventually drop below the number of available breeding sites, at which time the reproductive population will be limited by the relative availability of partners rather than density dependence. With too few available males, the reproductive output of the population will continue to decrease, ultimately leading to further population declines (see Fig. 4, Chapter 3).

Broader implications of the research

Rodents and climate change

The findings of this study have several broad implications. From a conservation perspective, perhaps the most concerning outcome of this study, as examined in Chapter 2, is the confirmation that invasive rodents impacts are increasing in response to ameliorating conditions brought about by climate change. Given the presence of rodents on the majority of the world's islands (Atkinson, 1985), and their proven ability to effect ecosystem change and species extinctions (Towns et al., 2006), such responses are likely to have substantial consequences for many insular species. The threat is especially evident for islands in more temperate regions such as the Southern Ocean, where most islands are showing a strong warming trend (Jones et al., 2003; Convey, 2006; Thost and Allison, 2006; le Roux and McGeoch, 2008; Cook et al., 2010; Lebouvier et al., 2011) and where the largest temperature changes are forecast to occur (Turner et al., 2007). This study also highlights the mounting evidence that mice are capable of initiating whole-island ecosystem change. Especially on islands such as most of those in the Southern Ocean where nutrient cycling is highly reliant on invertebrates (Smith and Steenkamp, 1992), mice must be given equal consideration as other invasive mammals when considering eradication for island restoration.

Land-sea interactions

The effects of penguin declines on sheathbill ecology documented in Chapter 3 provide an example of how most ecosystems are not closed, but rather closely linked to other spatially-connected systems through energy and nutrient flow (Helfield and Naiman, 2001; Schindler and Scheuerell, 2002; Chapin et al., 2011). Some of the most compelling evidence of coupled habitats comes from the land-sea interactions found in insular systems, where a significant percentage of nutrients are introduced through the excrement, food scraps, and carrion of marine visitors, especially seabirds (Anderson and Polis, 1999; Stapp et al., 1999; Towns et al., 2009). Consequently, while in many regards island food webs are relatively simple (Elton, 1958; Holt, 1996; Takimoto et al., 2008), they are strongly influenced by the complex marine systems underlying them.

The global decline in many penguin species, including rockhoppers, has been closely linked to widespread changes in the Southern Ocean brought on by climate change (Forcada and Trathan, 2009; Trivelpiece et al., 2011; Dehnhard et al., 2013). Thus while it has been demonstrated in this study that changes in sheathbill ecology are directly related to penguin

declines, the relationship has been greatly simplified. In reality the observed changes in sheathbills are partially the outcome of numerous and highly complex factors interacting on several spatial and temporal scales beginning with climate change and its physical effects on the Southern Ocean (Rayner et al., 2003; Parkinson, 2004; Whitehouse et al., 2008), and extending to the subsequent impacts on primary productivity and the abundance and distribution of krill (Atkinson et al., 2004; Massom et al., 2006; Ross et al., 2008; Flores et al., 2012), which in turn dictates the breeding, survival, and interactions of many top predators including penguins (Trivelpiece et al., 2011; Trathan et al., 2012; Dehnhard et al., 2013). Thus, factors as far removed as sea surface temperature and winter ice coverage in Antarctica, which greatly determine the abundance and distribution of krill stocks which in turn influence all populations further up the trophic ladder such as penguins (Flores et al., 2012), ultimately help determine the size of the reproductive population in sheathbills on Marion Island. Acknowledging that such far-reaching relationships are possible and accounting for the ability of global change to resonate across multiple ecosystems is therefore vital to understanding how species will respond to human impacts, on islands and in general. It also further reinforces the notion that ecosystems are highly integrated (Polis and Strong, 1996), and cannot be managed separately (Christensen et al., 1996; Chown and Froneman, 2008).

Focus on island endemics

There is need for greater study of island species, as for even relatively well-studied taxa such as birds many aspects of ecology remain significantly less studied when compared to species occurring on continents (Brooks et al., 2008; de Lima et al., 2011). For example, as demonstrated in Chapter 4, basal metabolic rate is a fundamental characteristic of all endotherms, yet only a handful of island birds have had their BMR measured, and fewer still to a level that allows intraspecific analysis. Islands are noted for their role in promoting evolutionary change, with species often undergoing a number of changes in order to persist. Greater focus on the ecology of endemic species may reveal additional adaptations to island living.

Further, human-mediated global change is certain to influence many species in profound and complex ways. However, any measure of change in a system must be understood or evaluated against a well-defined benchmark. The long-term changes

observed in sheathbills make clear the need for improved documentation and study of island species as many of the responses observed in this study are significant but subtle and would not have been evident without detailed knowledge of species ecology and vital rates. Giving greater focus to insular biota is imperative to understanding their current status and ecology as well as establishing a barometer against which further global change can be measured and mitigation measures evaluated.

Management implications

Invasive house mice

Given the significant and increasing ecological impact of invasive house mice on Marion Island, eradication is the only management strategy with the ability to protect and restore the island's ecosystem. Whilst mouse suppression through biological controls such as immunocontraceptive vaccines have been suggested (Jackson and van Aarde, 2003), such methods have thus far have proven highly problematic for wild mouse populations (Saunders et al., 2010). Further, control alone is unlikely to aid in ecosystem restoration, as even low rodent densities can inhibit the recovery of invertebrate populations (St Clair, 2011).

Eradication is an acceptable management option only if the adverse effects of such a program do not outweigh the benefits of pest removal (Myers et al., 2000; Courchamp et al., 2003) and environmental contamination and deleterious effects on non-target species are concerns for any eradication program. Large-scale rodent eradications employ the aerial broadcast of poison bait pellets, the most common of which is the second-generation (single dose required) anticoagulant brodifacoum (Howald et al., 2007), a highly lethal 4-hydroxycoumarin vitamin K antagonist poison. The main advantages of brodifacoum are that while it is safe for human use (the antidote is vitamin K and easily obtained), it is extremely toxic to rodents (Fisher and Fairweather, 2006). The potential for groundwater and surface water contamination from the poison is low (Ogilvie et al., 1997) and unlikely to contaminate water systems. Brodifacoum binds to organic matter when released, becomes inert and is slowly degraded by soil microorganisms over a period of 3-6 months (Fisher and Fairweather, 2006). While a wide variety of terrestrial invertebrates have been shown to ingest brodifacoum pellets, there are no records of lethal impacts (Hoare and Hare, 2006) and they are considered to be of low risk considering they have blood clotting systems unlike

vertebrates (Srimal, 1996). However, brodifacoum poses a substantial risk to non-target vertebrates in the form of first and secondary poisoning. For example, nontarget mortality from brodifacoum poisoning associated with the Macquarie Island Eradication Program included sub-Antarctic skuas (*Catharacta antarctica lonnbergi* Mathews), southern giant petrels (*Macronectes giganteus* Gmelin), and significant proportions of both the northern giant petrel (*Macronectes halli* Mathews) and kelp gull (*Larus dominicanus* Lichtenstein) populations (Anonymous, 2010). In this regard the use of brodifacoum could pose a serious barrier to mouse eradication on Marion Island.

Sheathbills, in addition to giant petrels, kelp gulls, and sub-Antarctic skuas, would assuredly be susceptible to poisoning. Preliminary captive trials have suggested primary poisoning poses low risk to sheathbills (Wanless et al., 2010). However, sheathbills are opportunistic hunters and consumers of mice and scavengers of any species, including other sheathbills (G.T.W. McClelland, personal observation). Brodifacoum persists in organs and tissue for up to six months (Eason et al., 2002), which strongly suggests that without proper management, mouse eradication would be synonymous with sheathbill eradication. Few viable alternatives to brodifacoum currently exist. Other second-generation anticoagulants hold no significant advantage over brodifacoum (Eason and Ogilvie, 2009) and first-generation (multiple dose required) anticoagulants, while less toxic, have been found ineffective against mice (Fisher, 2005). Also problematic are non-anticoagulant poisons such as zinc phosphide (less effective when wet and more toxic to avifauna than mammals; Eason and Ogilvie, 2009) and sodium monofluoroacetate (also known as 1080, detected and avoided by mice, highly soluble in water; Kaukeinen et al., 2000). A promising alternative poison may be cholecalciferol (vitamin D_3), which has low toxicity to birds (Eason et al., 2000) and been proven effective against mice in preliminary field trials in New Zealand (Hix et al., 2012). However, it has yet to be tested for aerial application or used independently in large-scale eradication efforts.

In lieu of a practical alternative to brodifacoum, an uncommon but feasible solution to poisoning concerns is live capturing and temporarily holding species at risk (Merton et al., 2002; Howald et al., 2007). With sheathbills, such an operation may be successful, as they have proven to be adaptable to captivity (Kidder, 1875; Wanless et al., 2010). However, the number of captured individuals required to maintain the genetic integrity of the population must first be determined. Also, considering sheathbills must be housed solitarily or as

breeding pairs (Kidder, 1875), and for up to several months, such an operation may be a significant undertaking.

Though a mouse eradication program on Marion Island is not without its challenges, few logistical barriers appear insurmountable. Further, the strict quarantine regulations already in place on the island (Anonymous, 1996) suggest that the risk of reinvasion would be minimal. While removing a species from an ecosystem may have unanticipated and unwanted consequences (D'Antonio and Vitousek, 1992; Courchamp et al., 1999; Bergstrom et al., 2009), mice are not known to control or compete with other alien species present on Marion Island and the risk of negative cascading effects from their removal would appear minimal. However, despite a previous highly successful cat eradication program on the island (Bester et al., 2000), the prospect of eliminating mice has gained little traction. This may be due to several factors including the failure up until this study to empirically demonstrate the ecosystem-level impacts of mice and the prospect for increasing damage. However, the foremost reason is undoubtedly the anticipated high financial cost and considerable risk of failure of such a program. In general the costs of eradication programs increase with island size and isolation (Martins et al., 2006), but accurate cost estimates are a complex process that can be influenced by a number of factors (Donlan and Wilcox, 2007) and therefore only expert opinion can give an accurate estimate for Marion Island. However, considering the island's considerable size and isolation (29 035 ha, 2 300 km from the nearest airport) the cost will almost certainly be higher than the $6.2 - $7.6M USD estimated for eradicating mice on Gough Island (6 500 ha, 2 400 km from nearest airport, McCarthy, 2013), and could conceivably reach or exceed the $25.7M budgeted for the multi-species eradication on Macquarie Island (12 780 ha, 1 500 km from nearest airport, Springer, 2011).

Further, despite an ever-increasing success rate of island eradications in general, at least one quarter of all attempted mouse eradications have failed (MacKay et al., 2007; Keitt et al., 2011), with a global failure rate considerably higher than that of other commensal rodent species such as Norway (*Rattus norvegicus* Berkenhout) and ship rats (*Rattus rattus* Linnaeus; Howald et al., 2007). Marion Island is considerably larger than the largest confirmed mouse eradication (Enderby Island, 710 ha; Torr, 2002), and still twice as large as Macquarie Island should that eradication effort prove successful. The probability of failure increases with island size (Howald et al., 2007), presumably making Marion Island one of the most challenging eradications to date.

Clearly the cost and risks of mouse eradication on Marion Island are difficult to predict, but have the potential to be considerable. Such obstacles are forecast to improve over time. In addition to the aforementioned islands, large-scale rodent eradication campaigns are currently underway or in the planning stages for the Aleutian Islands (Alaska), South Georgia, Ascension, and Tristan da Cunha islands (UK Overseas Territories), Lord Howe Island (Australia), the Queen Charlotte Islands (Canada), and the Antipodes Islands (New Zealand), among others. The knowledge gained from such efforts will undoubtedly improve the efficiency of such programs. However, even with the risks and costs associated with island eradications lowered they are likely to remain substantial. With limited fiscal resources, political and social obstacles are likely to remain as it may prove difficult to demonstrate to the South African public the cost-benefit of eradicating mice from an island many may have little awareness of and fewer still will have the privilege to visit. Increased awareness through the continued research of mouse effects may be beneficial towards this end. Greater support may also be garnered if mouse attacks on more charismatic fauna such as albatross continue to increase (Jones and Ryan, 2009). While such a turn of events would be unfortunate, a silver lining may be increased public awareness and support as well as improved prospects for enrolling the help of non-governmental organizations and/or subsidizing an eradication through private donations. However, barring the substantial financial assistance from such sources, it is likely mice will continue to persist on Marion Island for the foreseeable future.

Black-faced sheathbills

One of the primary goals of conservation is to promote the long-term survival of species and populations. Population persistence relies to a great extent on the number of breeding individuals therein, which must be large enough to maintain the population under various stochasticities and calamities (Shaffer, 1981). Thus, any decline in a small population increases its risk of extinction (Pimm et al., 1988; Purvis et al., 2000; Traill et al., 2010) and efforts should be made to sustain species numbers if possible. For sheathbills on Marion Island, population models indicate that the species is currently in decline. Moreover, the population will decline further under the likely scenario of increased rockhopper penguin losses. Management options for the sheathbill population appear limited as reversing or preventing further penguin declines are beyond the scope of anything less than a global conservation effort (Boersma, 2008). The eradication of mice from the island in the near

future appears unlikely, and it is also unclear to what extent such an effort would benefit sheathbills. Increases in invertebrate biomass following the removal of mice may provide more sheathbill foraging options and improve winter body condition. However, the time frame required for such improvements to become significant for sheathbills, and the size of the impact on vital rates are difficult to predict. Additionally, any benefit of increased invertebrate biomass may be outweighed by further penguin declines. Offspring sex ratio manipulation through supplemental feeding to increase the size of the reproductive population has proven to be an effective conservation tool for very small populations (Robertson et al., 2006; Lenz et al., 2007). However, its feasibility for a population as large as that of sheathbills on Marion Island is highly questionable. Such programs also carry some risk and have high potential for unforeseen problems (Powlesland and Lloyd, 1994; Clout et al., 2002; Wedekind, 2002).

One simple management option that may ameliorate declines in the sheathbill population is the introduction of artificial nesting sites, as suitable breeding habitat is the limiting factor in king penguin colonies (Burger, 1979). Though the number of king penguins breeding on the island in any given year is approximately 65 000 (Crawford et al., 2009), only *c*. 200 sheathbill pairs breed amongst them. Nest boxes are an effective conservation measure for many cavity-nesting species where suitable nesting sites are the limiting factor (Newton, 1994; Bolton et al., 2004; Libois et al., 2012) and their use in king penguin colonies has the potential to greatly increase the number of breeding sheathbill pairs. For example, the ability of nest boxes to aid in sheathbill population recovery after a 75 % decline in breeding sites within rockhopper penguin colonies was tested using the population matrix model developed in Chapter 3. Introducing a total of 200 nest boxes into king penguin colonies was predicted to eventually increase the number of adult males by 99.6 % above that predicted without nest boxes (Fig. 2), with the strong caveat that vital rates did not change.

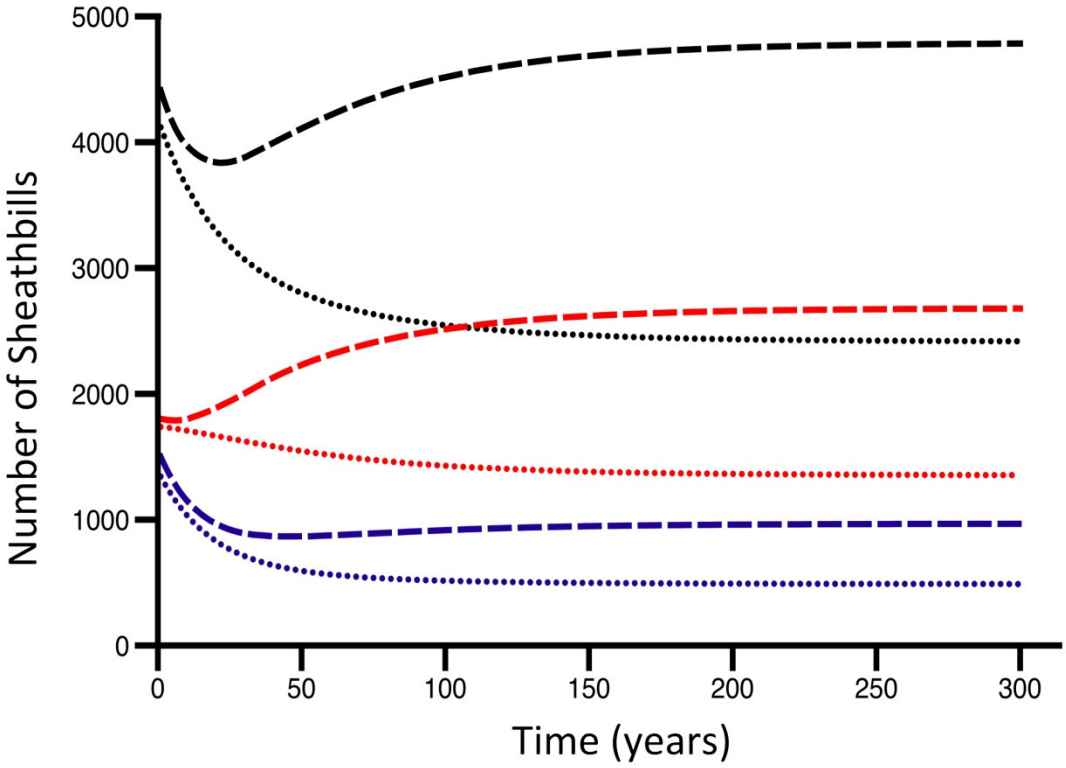


Figure 2: Sheathbill projected breeding population sizes over a 300-year time period on Marion Island under a 75 % reduction in breeding sites within rockhopper colonies. The dotted line represents the population without any form of management, and the dashed line represents the population with the addition of 200 nest boxes into king penguin colonies. Black lines refer to the absolute population size which includes juveniles, subadults, and adults. Red and blue lines refer to the number of adult females and males, respectively.

Nest boxes have the potential for negative impacts linked to density-dependent processes such as food limitation, and alteration of breeding behaviour (Møller, 1989; Pöysä and Pöysä, 2002; Mänd et al., 2005) and the ecology of the species must be considered carefully when designing such a program (Klein et al., 2007). Any management actions involving nest boxes for sheathbills should therefore proceed cautiously and be well-monitored. However, the high number of penguins suggests the risk of food limitation would be minimal, while the large size of the colonies would allow for adequate spacing to minimize adverse behavioural changes. Introducing sheathbill nest boxes is also unlikely to have a significantly negative impact on king penguins. A substantial floating population is

already present in the colonies and the increased energy demand associated with more breeders is unlikely to have a significant impact considering sheathbill kleptoparasitism has a negligible effect on penguins (Burger, 1981) and sheathbill predation on king penguin nestlings was not recorded during this study. Thus, nest boxes may be a viable option for increasing sheathbill numbers in the event of a decline.

Future work

Invasive house mice

In the absence of a mouse eradication program, several recommendations for future study are made.

- Though of great value, the sporadic nature of previous trapping efforts leaves many questions concerning mouse population dynamics on Marion Island unanswered. The one-year trapping programs in the 1980s and 1990s failed to document a complete annual cycle of population growth and decline, as the scheduled relief of personnel ensured that one-year trapping programs would begin in the middle of one population growth cycle and end before another could be completed. While this was less of an issue in 2008-11, only two full annual population cycles could be documented. Some small mammal populations, including house mice, show multiannual cyclic fluctuations in density, while others remain relatively stable (Korpimäki et al., 2004). It is yet unclear if the peak densities observed in this study represent typical years or fall somewhere on a fluctuating multiannual scale of high and low years. In a related matter, how factors such as weather and density dependence interact to regulate mouse populations is also poorly understood. It would thus be beneficial to continue the mouse capture-mark-recapture study for several consecutive years to explore the intrinsic and extrinsic factors that regulate Marion Island mouse population dynamics. Such a trapping program would ideally occur on a monthly basis and incorporate several replicates in the major habitat types.
- It would also be beneficial to improve our knowledge of mouse ecology from a whole-island perspective. Thus, any study program should incorporate fellfield habitat which was not considered in this study. Though mouse densities are likely to be the lowest of any of the major habitats (Gleeson, 1981), fellfield represents a considerable portion of the island (Gremmen and Smith, 2008) and mice have been demonstrated to have

significant landscape-level impacts in these areas (Phiri et al., 2008). Additionally, all knowledge of mouse densities on Marion Island is limited to coastal areas. Densities undoubtedly vary attitudinally and higher elevations may be under a greater rate of change as the island continues to warm. Including additional elevations would therefore greatly expand our knowledge of mouse impacts on the island as a whole and how they are changing under a warming climate.

- While this study documented increased mouse populations as a result of earlier breeding, other changes are likely and should be explored. Foremost among these is field metabolic rate (FMR). Marion Island is unique amongst Southern Ocean islands with invasive rodents, in that FMR has previously been quantified (Rowe-Rowe et al., 1989). Ameliorating temperatures are likely to depress the metabolic costs of thermoregulation in mice and other rodents on Southern Ocean islands. However, this remains unexplored and may be offset by declining prey resources. Increased survival and greater reproductive effort are also potential responses to ameliorating conditions, but remain unquantified.

Black-faced sheathbills

As sheathbills are a long-lived species, a long-term research program following the demographic monitoring in this study would be the most effective way to ensure their conservation (Wooller et al., 1992). Doing so would allow the examination of environmental and demographic stochasticity, as well as the ability to address age-specific questions. In the absence of such a program, several recommendations are made.

- Annual sheathbill surveys which include the recording of habitat use should continue, using multiple independent observers. On a long-term basis, attempts should also be made to estimate the adult sex ratio at regular intervals, allowing for the estimation of the reproductive population.
- It would be useful to further examine the relationship between sheathbill body condition and offspring sex ratio as this study was not designed to determine at which stage the bias occurred. Testing the primary sex ratio of sheathbills would yield greater insight into how birds regulate breeding in response to reduced habitat quality. Further, supplemental feeding experiments could address where sheathbills fall on the scale of income and capital breeders (Stephens et al., 2009). In addition to contributing to life

history theory, such an experiment could determine sheathbill reliance on body stores for egg production, and thus the degree to which changes in offspring sex ratio are driven by the loss of terrestrial invertebrates in winter and rockhopper penguins during the breeding season.

- Knowledge of sheathbill genetic diversity should be made a priority. Such small and isolated populations are susceptible to a number of genetic risks. Limited mating opportunities may lead to an increased frequency of matings between relatives, reducing the population's mean fitness through inbreeding depression (Briskie and Mackintosh, 2004). Moreover, the loss or fixation of alleles as a result of genetic drift reduces genetic variation and therefore the population's evolutionary potential (Keller and Waller, 2002) and this may have a significant effect on future adaptability to environmental change (Spielman et al., 2004; Allendorf et al., 2013). The genetic diversity of both Prince Edward Islands sheathbill populations should therefore be a matter of concern. Further, in the event of a mouse eradication campaign on Marion Island, a founder population of sheathbills may have to be taken into temporary captivity to be used for restocking the island (Wanless et al., 2010). Such an undertaking would require a detailed knowledge of sheathbill genetics to calculate the number of individuals necessary for the maintenance of genetic diversity within the population. Failure to account for both genetic diversity and gene flow could result in both founding (Groombridge et al., 2000; Briskie and Mackintosh, 2004; Jamieson, 2010) and sequential bottleneck events (Pruett and Winker, 2005; Taylor and Jamieson, 2008) that can erode genetic diversity. The genetic differences between Prince Edward Island and Marion Island should also be quantified. Doing so could answer a number of questions including the level of movement, if any, between the populations and if they should be considered separate conservation units. It could also determine the potential for the two populations to supplement one another as a management option in the event of a significant population loss, either through a natural catastrophe or induced by a mouse eradication effort on Marion Island. Finally, a growing body of evidence suggests that intraspecific variation in basal metabolic rate (BMR) has a strong genetic component (Ksiazek et al., 2004; Rønning et al., 2007; Tieleman et al., 2009; Konarzewski and Książek, 2012). Considering this study observed significant variation in BMR between two sympatric groups of sheathbills, knowledge of sheathbill genetics would be of great value in determining to what extent intraspecific variation in BMR reflects adaptation and phenotypic plasticity, respectively.

References

Allendorf, F.W., Luikart, G., Aitken, S.N., 2013. Conservation and the genetics of populations, 2nd ed. Wiley-Blackwell, Oxford.

Anderson, W.B., Polis, G.A., 1999. Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. Oecologia 118, 324–332.

Anonymous, 1996. Prince Edward Islands Management Plan. Department of Environmental Affairs and Tourism, Pretoria.

Anonymous, 2010. Macquarie Island non target bird mortality, specifically in relation to giant petrels - interim report. (Australia) Department of Primary Industries, Parks, Water and Environment, Biodiversity Monitoring Section, Resource Management and Conservation Divis.

Atkinson, A., Siegel, V., Pakhomov, E., Rothery, P., 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. Nature 432, 100–103.

Atkinson, I.A.E., 1985. The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifaunas, in: Moors, P.J. (Ed.), Conservation of Island Birds. Cambridge: International Council for Bird Preservation Technical Publication No. 3, pp. 35–81.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., Courchamp, F., 2012. Impacts of climate change on the future of biodiversity. Ecology Letters 15, 365–377.

Bergstrom, D.M., Lucieer, A., Kiefer, K., Wasley, J., Belbin, L., Pedersen, T.K., Chown, S.L., 2009. Indirect effects of invasive species removal devastate World Heritage Island. Journal of Applied Ecology 46, 73–81.

Bester, M.N., Bloomer, J.P., Bartlett, P.A., Muller, D.D., van Rooeyn, M., Buchner, H., 2000. Final eradication of feral cats from sub-Antarctic Marion Island, southern Indian Ocean. South African Journal of Wildlife Research 30, 53–57.

Boersma, P.D., 2008. Penguins as marine sentinels. BioScience 58, 597–607.

Bolton, M., Medeiros, R., Hothersall, B., Campos, A., 2004. The use of artificial breeding chambers as a conservation measure for cavity-nesting procellariiform seabirds: a case study of the Madeiran storm petrel (*Oceanodroma castro*). Biological Conservation 116, 73–80.

Briskie, J. V, Mackintosh, M., 2004. Hatching failure increases with severity of population bottlenecks in birds. Proceedings of the National Academy of Sciences of the U.S.A. 101, 558–561.

Brook, B.W., Sodhi, N.S., Bradshaw, C.J.A., 2008. Synergies among extinction drivers under global change. Trends in Ecology and Evolution 23, 453–460.

Brooks, T.M., Collar, N.J., Green, R.E., Marsden, S.J., Pain, D.J., 2008. The science of bird conservation. Bird Conservation International 18, S2–S12.

Burger, A.E., 1979. Breeding biology, moult, and survival of lesser sheathbills *Chionis minor* at Marion Island. Ardea 67, 1–14.

Burger, A.E., 1981. Time budgets, energy needs, and kleptoparasitism in breeding lesser sheathbills (*Chionis minor*). Condor 83, 106–112.

Chapin, F.S.I., Matson, P.A., Vitousek, P.M., 2011. Principles of terrestrial ecosystem ecology, 2nd ed. Springer, New York.

Chown, S.L., Convey, P., 2007. Spatial and temporal variability across life's hierarchies in the terrestrial Antarctic. Philosophical Transactions of the Royal Society B 362, 2307–2331.

Chown, S.L., Froneman, P.W., 2008. The Prince Edward Islands: land-sea interactions in a changing ecosystem. Sun Press, Stellenbosch.

Chown, S.L., Slabber, S., McGeoch, M.A., Janion, C., Leinaas, H.P., 2007. Phenotypic plasticity mediates climate change responses among invasive and indigenous arthropods. Proceedings of the Royal Society B 274, 2531–2537.

Christensen, N.L., Bartuska, A.M., Brown, J.H., Carpenter, S., Antonio, C.D., Francis, R., Franklin, J.F., Macmahon, J.A., Noss, R.F., Parsons, J., Peterson, C.H., Turner, M.G., Woodmansee, R.G., 1996. The report of the Ecological Society of America Committee on the scientific basis for ecosystem management. Ecological Applications 6, 665–691.

Clout, M.N., Elliott, G.P., Robertson, B.C., 2002. Effects of supplementary feeding on the offspring sex ratio of kakapo: a dilemma for the conservation of a polygynous parrot. Biological Conservation 107, 13–18.

Convey, P., 2006. Antarctic climate change and its influences on terrestrial ecosystems, in: Bergstrom, D.M., Convey, P., Huiskes, A.H.L. (Eds.), Trends in Antarctic Terrestrial and Limnetic Ecosystems. Springer, Dordrecht, pp. 253–272.

Cook, A.J., Poncet, S., Cooper, A.P.R., Herbert, D.J., Christie, D., 2010. Glacier retreat on South Georgia and implications for the spread of rats. Antarctic Science 22, 255–263.

Courchamp, F., Chapuis, J., Pascal, M., 2003. Mammal invaders on islands: impact, control and control impact. Biological Reviews 78, 347–383.

Courchamp, F., Langlais, M., Sugihara, G., 1999. Cats protecting birds: modelling the mesopredator release effect. Journal of Animal Ecology 68, 282–292.

Crain, C.M., Kroeker, K., Halpern, B.S., 2008. Interactive and cumulative effects of multiple human stressors in marine systems. Ecology Letters 11, 1304–1315.

Crawford, R.J.M., Whittington, P.A., Upfold, L., Ryan, P.G., Petersen, S.L., Dyer, B.M., Cooper, J., 2009. Recent trends in numbers of four species of penguins at the Prince Edward Islands. African Journal of Marine Science 31, 419–426.

Cunningham, D.M., Moors, P.J., 1994. The decline of rockhopper penguins *Eudyptes chrysocome* at Campbell Island, Southern Ocean and the influence of rising sea temperatures. Emu 94, 27–36.

D'Antonio, C.M., Vitousek, P.M., 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23, 63–87.

Dehnhard, N., Poisbleau, M., Demongin, L., Ludynia, K., Lecoq, M., Masello, J.F., Quillfeldt, P., 2013. Survival of rockhopper penguins in times of global climate change. Aquatic Conservation: Marine and Freshwater Ecosystems DOI: 10.1002/aqc.2331.

Didham, R.K., Tylianakis, J.M., Gemmell, N.J., Rand, T.A., Ewers, R.M., 2007. Interactive effects of habitat modification and species invasion on native species decline. Trends in Ecology and Evolution 22, 489–496.

Donlan, C.J., Wilcox, C., 2007. Complexities of costing eradications. Animal Conservation 10, 154–156.

Dukes, J.S., Mooney, H.A., 1999. Does global change increase the success of biological invaders? Trends in Ecology and Evolution 14, 135–139.

Eason, C.T., Murphy, E.C., Wright, G.R.G., Spurr, E.B., 2002. Assessment of risks of brodifacoum to non-target birds and mammals in New Zealand. Ecotoxicology 11, 35–48.

Eason, C.T., Ogilvie, S., 2009. A re-evaluation of potential rodenticides for aerial control of rodents. (New Zealand) Department of Conservation Science Internal Series 312, 1–33.

Eason, C.T., Wickstrom, M.L., Henderson, R., Milne, L., Arthur, D., 2000. Non-target and secondary poisoning risks associated with cholecalciferol, in: Proceedings of the New Zealand Plant Protection Conference. pp. 299–304.

Elton, C.S., 1958. The ecology of invasions by animals and plants. University of Chicago Press, Chicago.

Fisher, P., 2005. Review of house mouse (*Mus musculus*) susceptibility to anticoagulant poisons. (New Zealand) Department of Conservation Science Internal Series 198, 1–19.

Fisher, P., Fairweather, A., 2006. Brodifacoum: a review of current knowledge. (New Zealand) Department of Conservation Pesticide Information Reviews. Part 6. No. HAMRO-106522.

Flores, H., Atkinson, A., Kawaguchi, S., Krafft, B.A., Milinevsky, G., Nicol, S., Reiss, C., Tarling, G.A., Werner, R., Bravo Rebolledo, E., Cirelli, V., Cuzin-Roudy, J., Fielding, S., van Franeker, J.A., Groeneveld, J.J., Haraldsson, M., Lombana, A., Marschoff, E., Meyer, B.,

Pakhomov, E.A., Van de Putte, A.P., Rombolá, E., Schmidt, K., Siegel, V., Teschke, M., Tonkes, H., Toullec, J.Y., Trathan, P.N., Tremblay, N., Werner, T., 2012. Impact of climate change on Antarctic krill. Marine Ecology Progress Series 458, 1–19.

Forcada, J., Trathan, P.N., 2009. Penguin responses to climate change in the Southern Ocean. Global Change Biology 15, 1618–1630.

Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W., Holt, R.D., 2010. A framework for community interactions under climate change. Trends in Ecology and Evolution 25, 325–331.

Gleeson, J.P., 1981. Ecology of the house mouse *Mus musculus* Linnaeus, on Marion Island. MSc. thesis, University of Pretoria, South Africa.

Gremmen, N.J.M., Smith, V.R., 2008. Terrestrial vegetation and dynamics, in: Chown, S.L., Froneman, P.W. (Eds.), The Prince Edward Islands: Land-sea Interactions in a Changing Ecosystem. Sun Press, Stellenbosch, pp. 215–244.

Groombridge, J.J., Jones, C.G., Bruford, M.W., Nichols, R.A., 2000. “Ghost” alleles of the Mauritius kestrel. Nature 403, 616.

Helfield, J.M., Naiman, R.J., 2001. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. Ecology 82, 2403–2409.

Hellmann, J.J., Byers, J.E., Bierwagen, B.G., Dukes, J.S., 2008. Five potential consequences of climate change for invasive species. Conservation Biology 22, 534–543.

Hix, S., Aylett, P., Shapiro, L., Macmorran, D., Eason, C.T., Ross, J.G., Miller, A., Ogilvie, S.C., 2012. Low-dose cholecalciferol bait for possum and rodent control. New Zealand Journal of Agricultural Research 55, 37–41.

Hoare, J.M., Hare, K.M., 2006. The impact of brodifacoum on non-target wildlife: gaps in knowledge. New Zealand Journal Of Ecology 30, 157–167.

Holt, R.D., 1996. Food webs in space: an island biogeographic perspective, in: Polis, G.A., Winemiller, K.O. (Eds.), Food Webs: Integration of Pattern and Process. Chapman & Hall, London, pp. 313–323.

Howald, G., Donlan, C.J., Glavan, J.P., Russell, J.C., Parkes, J., Samaniego, A., Wang, Y., Veitch, D., Genovesi, P., Pascal, M., Saunders, A., Tershy, B., 2007. Invasive rodent eradication on islands. Conservation Biology 21, 1258–1268.

Jackson, T.P., van Aarde, R.J., 2003. Advances in vertebrate pest control: implications for the control of feral house mice on Marion Island. South African Journal of Science 99, 130–136.

Jamieson, I.G., 2010. Founder effects, inbreeding, and loss of genetic diversity in four avian reintroduction programs. Conservation Biology 25, 115–123.

Jones, A.G., Chown, S.L., Ryan, P.G., Gremmen, N.J.M., Gaston, K.J., 2003. A review of conservation threats on Gough Island: a case study for terrestrial conservation in the Southern Oceans. Biological Conservation 113, 75–87.

Jones, M.G.W., Ryan, P.G., 2009. Evidence of mouse attacks on albatross chicks on sub-Antarctic Marion Island. Antarctic Science 22, 39–42.

Kaukeinen, D.E., Spragins, C., Hobson, J., 2000. Risk-benefit considerations in evaluating commensal anticoagulant rodenticide impacts to wildlife. Proceedings of the Vertebrate Pest Conferance 19, 245–256.

Keitt, B., Campbell, K., Saunders, A., Clout, M., Wang, Y., Heinz, R., Newton, K., Tershy, B., Conservation, I., Cruz, S., Centre, W.M., Species, I., Group, S., Campus, T., Bag, P., 2011. The Global Islands Invasive Vertebrate Eradication Database: a tool to improve and facilitate restoration of island ecosystems, in: Veitch, C.R., Clout, M.N. (Eds.), Island Invasives: Eradication and Management. IUCN, Gland, Switzerland, pp. 74–77.

Keller, L.F., Waller, D.M., 2002. Inbreeding effects in wild populations. Trends in Ecology and Evolution 17, 230–241.

Kidder, J.H., 1875. Birds of Kerguelen Island. Bulletin of the American Museum of Natural History 2, 1–51.

Klein, Á., Nagy, T., Csörgő, T., Mátics, R., 2007. Exterior nest-boxes may negatively affect barn owl *Tyto alba* survival: an ecological trap. Bird Conservation International 17, 263–271.

Konarzewski, M., Książek, A., 2012. Determinants of intra-specific variation in basal metabolic rate. Journal of Comparative Physiology B 183, 27–41.

Korpimäki, E., Brown, P.R., Jacob, J., Pech, R.P., 2004. The puzzles of population cycles and outbreaks of small mammals solved? Bioscience 54, 1071–1079.

Ksiazek, A., Konarzewski, M., Lapo, I.B., 2004. Anatomic and energetic correlates of divergent selection for basal metabolic rate in laboratory mice. Physiological and Biochemical Zoology 77, 890–899.

Lebouvier, M., Laparie, M., Hullé, M., Marais, A., Cozic, Y., Lalouette, L., Vernon, P., Candresse, T., Frenot, Y., Renault, D., 2011. The significance of the sub-Antarctic Kerguelen Islands for the assessment of the vulnerability of native communities to climate change, alien insect invasions and plant viruses. Biological Invasions 13, 1195–1208.

Lenz, T.L., Jacob, A., Wedekind, C., 2007. Manipulating sex ratio to increase population growth: the example of the lesser kestrel. Animal Conservation 10, 236–244.

Libois, E., Gimenez, O., Oro, D., Mínguez, E., Pradel, R., Sanz-Aguilar, A., 2012. Nest boxes: A successful management tool for the conservation of an endangered seabird. Biological Conservation 155, 39–43.

De Lima, R.F., Bird, J.P., Barlow, J., 2011. Research effort allocation and the conservation of restricted-range island bird species. Biological Conservation 144, 627–632.

MacKay, J.W.B., Russell, J.C., Murphy, E.C., 2007. Eradicating house mice from islands: successes, failures, and the way forward, in: Fagerstone, K.A., Witmer, G.W. (Eds.), Managing Vertebrate Invasive Species: Proceedings of an International Symposium. United States Department of Agriculture, Fort Collins, CO, pp. 294–304.

Mänd, R., Tilgar, V., Lõhmus, A., Leivits, A., 2005. Providing nest boxes for hole-nesting birds – does habitat matter? Biodiversity and Conservation 14, 1823–1840.

Martins, T.L.F., Brooke, M.D.L., Hilton, G.M., Farnsworth, S., Gould, J., Pain, D.J., 2006. Costing eradications of alien mammals from islands. Animal Conservation 9, 439–444.

Massom, R.A., Stammerjohn, S.E., Smith, R.C., Pook, M.J., Iannuzzi, R.A., Adams, N., Martinson, D.G., Vernet, M., Fraser, W.R., Quetin, L.B., Ross, R.M., Massom, Y., Krouse, H.R., 2006. Extreme anomalous atmospheric circulation in the west Antarctic Peninsula region in austral spring and summer 2001/02, and its profound impact on sea ice and biota. Journal of Climate 19, 3544–3571.

McCann, K., 2007. Protecting biostructure. Nature 446, 29.

McCarthy, D.P., 2013. Costing conservation. Significance 10, 9–13.

Merton, D., Climo, G., Laboudallon, V., Robert, S., Mander, C., 2002. Alien mammal eradication and quarantine on inhabited islands in the Seychelles, in: Veitch, C.R., Clout, M.N. (Eds.), Turning the Tide: The Eradication of Invasive Species. IUCN Invasive Species Specialist Group, Gland, Switzerland, pp. 182–198.

Møller, A.P., 1989. Parasites, predators, and nest boxes: facts and artefacts in nest box studies of birds? Oikos 56, 421–423.

Mora, C., Metzger, R., Rollo, A., Myers, R.A., 2007. Experimental simulations about the effects of overexploitation and habitat fragmentation on populations facing environmental warming. Proceedings of the Royal Society B 274, 1023–1028.

Myers, J.H., Simberloff, D., Kuris, A.M., Carey, J.R., 2000. Eradication revisited: dealing with exotic species. Trends in Ecology and Evolution 15, 316–320.

Newton, I., 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review. Biological Conservation 70, 265–276.

Ogilvie, S.C., Pierce, R.J., Wright, G.R.G., Booth, L.H., Eason, C.T., 1997. Brodifacoum residue analysis in water, soil, invertebrates, and birds after rat eradication on Lady Alice Island. New Zealand Journal Of Ecology 21, 195–197.

Parkinson, C.L., 2004. Southern Ocean sea ice and its wider linkages: insights revealed from models and observations. Antarctic Science 16, 387–400.

Phiri, E.E., McGeoch, M.A., Chown, S.L., 2008. Spatial variation in structural damage to a keystone plant species in the sub-Antarctic: interactions between *Azorella selago* and invasive house mice. Antarctic Science 21, 189–196.

Pimm, S.L., Jones, H.L., Diamond, J., 1988. On the risk of extinction. American Naturalist 132, 757–785.

Polis, G.A., Strong, D.R., 1996. Food web complexity and community dynamics. American Naturalist 147, 813–846.

Powlesland, R.G., Lloyd, B.D., 1994. Use of supplementary feeding to induce breeding in free-living kakapo *Strigops habroptilus* in New Zealand. Biological Conservation 69, 97–106.

Pöysä, H., Pöysä, S., 2002. Nest-site limitation and density dependence of reproductive output in the common goldeneye *Bucephala clangula*: implications for the management of cavity-nesting birds. Journal of Applied Ecology 39, 502–510.

Pruett, C.L., Winker, K., 2005. Northwestern song sparrow populations show genetic effects of sequential colonization. Molecular Ecology 14, 1421–1434.

Purvis, A., Gittleman, J.L., Cowlishaw, G., Mace, G.M., 2000. Predicting extinction risk in declining species. Proceedings of the Royal Society B 267, 1947–1952.

Rayner, N.A., Parker, D.E., Horton, E.B., Folland, C.K., Alaxander, L. V, Rowell, D.P., Kent, E.C., Kaplan, A., 2003. Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late nineteenth century. Journal of Geophysical Research 108, 4407, doi:10.1029/2002JD002670.

Robertson, B.C., Elliott, G.P., Eason, D.K., Clout, M.N., Gemmell, N.J., 2006. Sex allocation theory aids species conservation. Biology Letters 2, 229–231.

Rønning, B., Jensen, H., Moe, B., Bech, C., 2007. Basal metabolic rate: heritability and genetic correlations with morphological traits in the zebra finch. Journal of Evolutionary Biology 20, 1815–1822.

Ross, R.M., Quetin, L.B., Martinson, D.G., Iannuzzi, R.A., Stammerjohn, S.E., Smith, R.C., 2008. Palmer LTER: Patterns of distribution of five dominant zooplankton species in the epipelagic zone west of the Antarctic Peninsula, 1993–2004. Deep Sea Research Part II: Topical Studies in Oceanography 55, 2086–2105.

le Roux, P.C., McGeoch, M.A., 2008. Changes in climate extremes, variability and signature on sub-Antarctic Marion Island. Climatic Change 86, 309–329.

Rowe-Rowe, D.T., Green, B., Crafford, J.E., 1989. Estimated impact of feral house mice on Sub-Antarctic invertebrates at Marion Island. Polar Biology 9, 457–460.

Saunders, G., Cooke, B., McColl, K., Shine, R., Peacock, T., 2010. Modern approaches for the biological control of vertebrate pests: an Australian perspective. Biological Control 52, 288–295.

Schindler, D.E., Scheuerell, M.D., 2002. Habitat coupling in lake ecosystems. Oikos 98, 177–189.

Shaffer, M.L., 1981. Minimum for species population sizes for species conservation. Bioscience 31, 131–134.

Smith, V.R., Steenkamp, M., 1992. Soil macrofauna and nitrogen on a sub-Antarctic island. Oecologia 92, 201–206.

Sorte, C.J.B., Ibáñez, I., Blumenthal, D.M., Molinari, N.A., Miller, L.P., Grosholz, E.D., Diez, J.M., D'Antonio, C.M., Olden, J.D., Jones, S.J., Dukes, J.S., 2013. Poised to prosper? A cross-system comparison of climate change effects on native and non-native species performance. Ecology Letters 16, 261–270.

Spielman, D., Brook, B.W., Frankham, R., 2004. Most species are not driven to extinction before genetic factors impact them. Proceedings of the National Academy of Sciences of the U.S.A. 101, 15261–15264.

Springer, K., 2011. Planning processes for eradication of multiple pest species on Macquarie Island – an Australian case study, in: Veitch, C.R., Clout, M.N., Towns, D.R. (Eds.), Island Invasives: Eradication and Management. IUCN, Gland, Switzerland, pp. 228–232.

Srimal, S., 1996. Blood clotting in invertebrates. Progress in Molecular and Subcellular Biology 15, 88–100.

St Clair, J.J.H., 2011. The impacts of invasive rodents on island invertebrates. Biological Conservation 144, 68–81.

Stachowicz, J.J., Terwin, J.R., Whitlatch, R.B., Osman, R.W., 2002. Linking climate change and biological invasions: Ocean warming facilitates nonindigenous species invasions. Proceedings of the National Academy of Sciences of the U.S.A. 99, 15497–15500.

Stapp, P., Polis, G.A., Sánchez Piñero, F., 1999. Stable isotopes reveal strong marine and El Nino effects on island food webs. Nature 401, 1997–1999.

Stephens, P.A., Boyd, I.L., McNamara, J.M., Houston, A.I., 2009. Capital breeding and income breeding: their meaning, measurement, and worth. Ecology 90, 2057–2067.

Takimoto, G., Spiller, D.A., Post, D.M., 2008. Ecosystem size, but not disturbance, determines food-chain length on islands of the Bahamas. Ecology 89, 3001–3007.

Taylor, S.S., Jamieson, I.G., 2008. No evidence for loss of genetic variation following sequential translocations in extant populations of a genetically depauperate species. Molecular Ecology 17, 545–556.

Thost, D., Allison, I., 2006. The climate of Heard Island, in: Green, K., Woehler, E. (Eds.), Heard Island: Southern Ocean Sentinel. Surrey, Beatty and Sons, Chipping Norton, Australia, pp. 52–68.

Tieleman, B.I., Versteegh, M.A., Fries, A., Helm, B., Dingemanse, N.J., Gibbs, H.L., Williams, J.B., 2009. Genetic modulation of energy metabolism in birds through mitochondrial function. Proceedings of the Royal Society B 276, 1685–1693.

Torr, N., 2002. Eradication of rabbits and mice from subantarctic Enderby and Rose Islands, in: Turning the Tide: The Eradication of Invasive Species. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland, pp. 319–328.

Towns, D.R., Atkinson, I.A.E., Daugherty, C.H., 2006. Have the harmful effects of introduced rats on islands been exaggerated? Biological Invasions 8, 863–891.

Towns, D.R., Wardle, D.A., Mulder, C.P.H., Yeates, G.W., Fitzgerald, B.M., Parrish, G.R., Bellingham, P.J., Bonner, K.I., 2009. Predation of seabirds by invasive rats: multiple indirect consequences for invertebrate communities. Oikos 118, 420–430.

Traill, L.W., Brook, B.W., Frankham, R.R., Bradshaw, C.J.A., 2010. Pragmatic population viability targets in a rapidly changing world. Biological Conservation 143, 28–34.

Trathan, P.N., Ratcliffe, N., Masden, E.A., 2012. Ecological drivers of change at South Georgia: the krill surplus, or climate variability. Ecography 35, 983–993.

Trivelpiece, W.Z., Hinke, J.T., Miller, A.K., Reiss, C.S., Trivelpiece, S.G., Watters, G.M., 2011. Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. Proceedings of the National Academy of Sciences of the U.S.A. 108, 7625–7628.

Turner, J., Overland, E., Walsh, J.E., 2007. An Arctic and Antarctic perspective on recent climate change. International Journal of Climatology 293, 277–293.

Walther, G., Roques, A., Hulme, P.E., Sykes, M.T., Pysek, P., Kühn, I., Zobel, M., Bacher, S., Botta-Dukát, Z., Bugmann, H., Czúcz, B., Dauber, J., Hickler, T., Jarosík, V., Kenis, M., Klotz, S., Minchin, D., Moora, M., Nentwig, W., Ott, J., Panov, V.E., Reineking, B., Robinet, C., Semenchenko, V., Solarz, W., Thuiller, W., Vilà, M., Vohland, K., Settele, J., 2009. Alien species in a warmer world: risks and opportunities. Evolution 24, 686–693.

Wanless, R.M., Cooper, J., Slabber, M., Ryan, P.G., 2010. Risk assessment of birds foraging terrestrially at Marion and Gough Islands to primary and secondary poisoning by rodenticides. Wildlife Research 37, 524–530.

Wedekind, C., 2002. Manipulating sex ratios for conservation: short-term risks and long-term benefits. Animal Conservation 5, 13–20.

Whitehouse, M.J., Meredith, M.P., Rothery, P., Atkinson, A., Ward, P., Korb, R.E., 2008. Rapid warming of the ocean around South Georgia, Southern Ocean, during the 20th century:

forcings, characteristics and implications for lower trophic levels. Deep Sea Research Part I 55, 1218–1228.

Willis, C.G., Ruhfel, B.R., Primack, R.B., Miller-Rushing, A.J., Losos, J.B., Davis, C.C., 2010. Favorable climate change response explains non-native species' success in Thoreau's woods. PloS one 5, e8878.

Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., Dormann, C.F., Forchhammer, M.C., Grytnes, J.-A., Guisan, A., Heikkinen, R.K., Høye, T.T., Kühn, I., Luoto, M., Maiorano, L., Nilsson, M.-C., Normand, S., Öckinger, E., Schmidt, N.M., Termansen, M., Timmermann, A., Wardle, D.A., Aastrup, P., Svenning, J.-C., 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. Biological Reviews 88, 15–30.

Wooller, R.D., Bradley, J.S., Croxall, J.P., 1992. Long-term population studies of seabirds. Trends in Ecology and Evolution 7, 111–114.

Appendix A: Input and R code for the matrix model used to estimate the impact of phenology on the Marion island mouse population (Chapter 2).

Abbreviations

s.j = monthly juvenile survival

s.s = monthly subadult survival

s.a = monthly adult survival

litsize = litter size (number of female pups produced)

n0 = starting density of each age class.

pb = percentage of females breeding. Also indicates breeding phenology.

Monthly apparent survival estimates from the top 1998-99 slope model pooled across replicates; {Phi(age*temp)P(icv)}. Red numbers are estimates for missing values.

	S-O	O-N	N-D	D-J	J-F	F-M	M-A	A-M	M-J	J-J	J-A	A-S
sj	0.318	0.564	0.747	0.754	0.852	0.842	0.836	0.666	0.544	0.418	0.418	0.408
ss	0.571	0.787	0.894	0.898	0.943	0.938	0.936	0.851	0.774	0.672	0.672	0.664
sa	0.571	0.787	0.894	0.898	0.943	0.938	0.936	0.851	0.774	0.672	0.672	0.664

Input (all models):

```
s.j<- c(0.318,0.564,0.747,0.754,0.852,0.842,0.836,0.666,0.544,0.418,0.418,0.408)
s.s<- c(0.571,0.787,0.984,0.898,0.943,0.938,0.936,0.851,0.774,0.672,0.672,0.664)
s.a<- c(0.571,0.787,0.984,0.898,0.943,0.938,0.936,0.851,0.774,0.672,0.672,0.664)
litsize <- 3.62
n0<- c(0,0,10.9)
#For breeding beginning in January (juveniles appear in February)
pb <-  c(0,0,0,0,0.84,0.84,0.52,0.52,0,0,0,0)
#For breeding beginning in December (juveniles appear in January)
pb <-  c(0,0,0,0.84,0.84,0.52,0.52,0.52,0,0,0,0)
#For breeding beginning in November (juveniles appear in December)
pb <-  c(0,0,0.84,0.84,0.52,0.52,0.52,0.52,0,0,0,0)

#Matrix Code:
A <- array(dim=c(3,3,12)) #set matrix dimensions
```

```
for(i in 1:12) A[,,i] <- matrix(c(0,0, pb[i]*litsize, s.j[i],0,0,0,s.s[i], s.a[i]), nrow=3, byrow=T)
n <- matrix(nrow=3, ncol=13)
n[,1] <- n0
for (i in 1:12) n[,i+1] = A[,,i]%*%n[,i]
n   #density estimate for each age class
```

Appendix B: Equations and R code for the two-part conditional model examining the relationship between invertebrate biomass and mouse density (Chapter 2).

For each invertebrate group in each vegetation type two data sets were created: one indicating whether the invertebrate group was present or not at each site, the other showing the log-transformed biomass for those sites where the invertebrate group was present. These two data sets are hereafter referred to as the "presence data" and "biomass given presence data", respectively. Both the presence data and the biomass given presence data were modelled in terms of the predictor variables, using logistic and ordinary regression, respectively. The logistic and ordinary regression models examining the relationship between invertebrate biomass and mouse destiny (biomass ~ mouse density) were then combined to model the expected invertebrate biomass in relation to mouse density. Specifically, let *Y*(*w*) be invertebrate biomass where *w* is the vector of mouse density and let *Z*(*x*) be the binary variable, equal to 1 when the invertebrate group is present and 0 when not, where *x* is the vector of mouse density. The expected value of *Y* is given by:

$$E(Y) = \Pr(Z = 1)\, E(Y|Z = 1) + \Pr(Z = 0)\, E(Y|Z = 0),$$
$$= \Pr(Z = 1)\, E(Y|Z = 1),$$
$$= \pi\mu$$

where π = Pr(Z = 1) and μ = E(Y | Z = 1). As shown by Stefánsson (1996) and Welsh et al. (1996), the estimate of the expected invertebrate biomass is computed as follows:

$$\hat{E}(Y) = \hat{\pi}\hat{\mu} \qquad \text{(equation 1)}$$

where

$$\hat{\pi} = \exp(x'\hat{\beta})/\{1 + \exp(x'\hat{\beta})\} \qquad \text{(equation 2)}$$

and

$$\hat{\mu} = \exp(w'\hat{\theta} + \hat{\sigma}^2/2) \qquad \text{(equation 3)}$$

are the estimates of π and μ obtained from the two regression models. Thus, $\hat{\beta}$ is the vector of estimates of the coefficients in the logistic regression model for the presence data, and *x* is the corresponding vector of explanatory variables. Similarly, $\hat{\theta}$ is the vector of estimates, *w* the vector of explanatory variables, and $\hat{\sigma}^2$ the residual mean square in the regression model for the log-biomass data (Crow and Shimizu, 1988).

The confidence interval for the estimate in equation 1 was calculated using parametric bootstrap methods as outlined in Fletcher et al. (2005). Alternative values of $\hat{E}(Y)$ were randomly generated by resampling β, θ, and σ and then used in equations 2 and

3. With these values, 100 000 bootstrap samples were taken. After sorting these values by magnitude, the 2.5th and 97.5th percentiles represent the lower and upper 95% confidence limit. Analyses were performed in the statistical software R and the package *MuMIn* (Barton, 2012).

R code for two-part conditional models (equations 1:3 in text) and confidence limits

Using soil worms in *A. magellanica* as an example, where ew_aca.txt is the data file, "mass" is invertebrate biomasss, and "smavg" is mouse density.

```
#Create inverse logit function
expit <- function(x) exp(x)/(1+exp(x))
#Read data
dat_ew_aca <- read.table("ew_aca.txt", header=T, sep="\t")
head(dat_ew_aca) ; tail(dat_ew_aca) ; summary(dat_ew_aca)
#Review histograms
hist(dat_ew_aca$mass)
hist(log(dat_ew_aca$mass+1))
hist(log(dat_ew_aca$mass[dat_ew_aca$mass>0]))
# 'presence' data set; mass as binary variable
dat.bin_ew_aca <- dat_ew_aca
dat.bin_ew_aca$mass[dat_ew_aca$mass>0] <- 1
# modelling presence
m.glm_ew_aca <- glm(mass ~ smavg, family=binomial, data=dat.bin_ew_aca)
summary(m.glm_ew_aca)
# modelling log-mass
m.la_ew_aca <- lm(log(mass[mass>0]) ~ smavg[mass>0], data=dat_ew_aca)
summary(m.la_ew_aca)
# predicting mean response (equations 1-3):
# the expit part is eq 2, i.e. inverse logit of the logistic regression
# the exp part is for the mass, eq 3
# generating 200 evenly spaced x values for which we want predictions to plot
x_ew_aca<- seq(min(dat_ew_aca$smavg), max(dat_ew_aca$smavg), length.out=200)
y_ew_aca<- expit(m.glm_ew_aca$coefficients[1] +
```

```
m.glm_ew_aca$coefficients[2]*x_ew_aca) * exp(m.la_ew_aca$coefficients[1] +
m.la_ew_aca$coefficients[2]*x_ew_aca + (summary(m.la_ew_aca)$sigma^2)/2)
# confidence intervals
# number of bootstrap replicates
nboot <- 100000
ucl_ew_aca <- lcl_ew_aca <- rep(NA, length(x_ew_aca))
j_ew_aca <- 1
# for every point on x, generate bootstrap samples and take the 2.5th and 97.5th quantiles
as confidence limits
for (i in x_ew_aca) {
# first choose nbooot random samples from the glm predictions; we have intercept and
slope,
# i.e. the vector of explanatory variables is c(1,i) and the betas are the coefficients
# the variance is calculated from the variance-covariance matrix as described in Fletcher et
al., (2005)
glmpart_ew_aca <- rnorm(nboot, m.glm_ew_aca$coefficients[1] +
m.glm_ew_aca$coefficients[2]*i,  sqrt(t(c(1, i)) %*% vcov(m.glm_ew_aca) %*%  c(1, i)))
# similar as above but for the lm part of the model
lmpart_ew_aca <- rnorm(nboot, m.la_ew_aca$coefficients[1] +
m.la_ew_aca$coefficients[2]*i,  sqrt( t(c(1, i)) %*% vcov(m.la_ew_aca) %*%  c(1, i)))
# lm part also requires sampling for the variance from a chi-square distribution
lmsigpart_ew_aca <- summary(m.la_ew_aca)$df[2]*summary(m.la_ew_aca)$sigma^2 /
rchisq(nboot, summary(m.la_ew_aca)$df[2])
# putting the pieces together according to equations 1-3
ys_ew_aca <- expit(glmpart_ew_aca) * exp(lmpart_ew_aca + lmsigpart_ew_aca/2)
lcl_ew_aca[j_ew_aca] <- quantile(ys_ew_aca, 0.025)          # lower confidence limit
ucl_ew_aca[j_ew_aca] <- quantile(ys_ew_aca, 0.975)          # upper confidence limit
j_ew_aca <- j_ew_aca+1
}
```

References

Fletcher, D., MacKenzie, D., Villouta, E., 2005. Modelling skewed data with many zeros: A simple approach combining ordinary and logistic regression. Environmental and Ecological Statistics 12, 45–54.

Appendix C: SECR Model Estimates (Chapter 2)

SECR model estimates of *g0* (the detection probability when the distance between the trap and an animal's home range center is 0) and σ (spatial scale relating to a species' home range width in meters), and model selection results. Lcl and ucl indicate the lower and upper 95 % confidence limits, respectively. The algorithm 'BFGS' was used to maximize the log likelihood in all models. Unless otherwise stated, all models used an exponential detection function. Parameters refer to the parameters of detection probability *g0* and σ. They are both assumed to be constant (the null model) unless otherwise stated. Effects on parameters of detection probability are specified as follows:

b learned response (the animal becomes trap happy)
B transient (Markovian) response (the animal becomes trap shy)
k site learned response (the trap site becomes more effective after any animal is caught)
K site transient response (the trap site becomes less effective after any animal is caught)
bk animal x site learned response (the animal becomes trap happy in relation to a particular trap)
Bk animal x site transient response (the animal becomes trap shy in relation to a particular trap)

Model selection was based on Akaike's Information Criterion adjusted for sample size (AICc), where a smaller value indicates a better model. ΔAICc is the difference in AICc between the current model and the best. AICc weights give the relative support each model has compared to the others, and k is the number of parameters in the model. Only the five highest ranking models with ΔAICc > 7 only are shown.

Mire 1991-92

Session 1, June 3-7*

	estimate	lcl	ucl

g0	0.347	0.187	0.549
σ	8.5	6.9	10.5

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~k	4	-459.5	927.9	0	0.3016
g0~k, *σ*~k	5	-458.4	928.2	0.262	0.2645
g0~K	4	-460.0	929.0	1.047	0.1787
σ~K	4	-460.8	930.5	2.632	0.0809
g0~K, *σ*~K	5	-460.0	931.4	3.501	0.0545

*4 mice removed

Session 2, August 1-5*

	estimate	lcl	ucl
g0	0.155	0.095	0.243
σ	8.8	8.7	9.0

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k, *σ*~k	5	-259.1	530.2	0	1

*1 mouse removed

Session 3, October 1-5*

	estimate	lcl	ucl
g0	0.201	0.072	0.449
σ	10.4	6.8	15.8

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
null	3	-196.0	399.7	0	0.1818
g0~b	4	-194.5	400.1	0.444	0.1456
g0~K	4	-194.5	400.1	0.481	0.1429

g0~k	4	-194.6	400.3	0.684	0.1291
σ~b	4	-194.8	400.6	0.980	0.1114

*1 mouse removed

Session 4, December 1-5*

	estimate	lcl	ucl
g0	0.034	0.017	0.068
σ	34.9	19.0	64.0

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
null	3	-137.8	286.4	0	0.8223
σ~b	4	-136.4	290.8	4.458	0.0885
σ~B	4	-136.7	291.4	5.029	0.0665

*halfnormal detection function used

Session 5, February 1-5*

	estimate	lcl	ucl
g0	0.146	0.074	0.267
σ	9.5	6.8	13.1

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
null	3	-245.7	498.414	0	0.2431
σ~B	4	-245.0	499.697	1.283	0.1280
σ~k	4	-245.2	500.104	1.690	0.1044
g0~K	4	-245.2	500.181	1.767	0.1005
g0~k	4	-245.3	500.318	1.904	0.0938

*1 mouse removed

Mire 1993-94

Session 1, May 3-7

	estimate	lcl	ucl
g0	0.067	0.046	0.098
σ	11.0	10.7	11.2

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~K, *σ*~K	5	-530.0	1070.7	0	1

Session 2, July 1-5*

	estimate	lcl	ucl
g0	0.060	0.036	0.099
σ	11.9	9.1	15.7

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~K	4	-554.3	1117.1	0	0.7319
g0~K	4	-555.3	1119.1	2.07	0.2600

*6 mice removed

Session 3, August 4-8*

	estimate	lcl	ucl
g0	0.038	0.021	0.069
σ	17.1	10.7	27.4

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~bk	4	-460.3	929.8	0	0.1608

σ~Bk	4	-460.3	929.3	0.104	0.1527
σ~B	4	-460.3	929.3	0.118	0.1516
g0~bk	4	-461.0	930.8	1.565	0.0735
null	3	-462.2	930.8	1.607	0.0720

*1 mouse removed

Session 4, September 3-7*

	estimate	lcl	ucl
g0	0.073	0.048	0.111
σ	10.3	10.1	10.5

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~K, *σ*~K	5	-500.7	1012.3	0	1

*5 mice removed

Session 5, October 3-7*

	estimate	lcl	ucl
g0	0.159	0.103	0.237
σ	9.2	9.1	9.4

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k *σ*~k	5	-482.5	976.0	0	1

*10 mice removed

Session 6, November 4-8*

	estimate	lcl	ucl

g0	0.216	0.084	0.451
σ	12.8	9.4	17.5

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~k	4	-394.0	797.1	0	0.7359
g0~k, *σ*~k	5	-393.9	799.4	2.246	0.2394
g0~k	4	-397.4	803.9	6.785	0.0247

*8 mice removed

Session 7, December 3-7*

	estimate	lcl	ucl
g0	0.110	0.057	0.203
σ	11.4	9.2	14.2

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k, *σ*~k	5	-251.8	516.4	0	0.5633
g0~K, *σ*~K	5	-252.1	516.9	0.509	0.4367

*3 mice removed

Session 8, January 1-5*

	estimate	lcl	ucl
g0	0.294	0.112	0.578
σ	8.7	5.6	13.5

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k	4	-182.9	377.3	0	0.2845
σ~k	4	-183.1	377.9	0.519	0.2195
g0~K	4	-183.4	378.5	1.124	0.1622
g0~B	4	-184.1	379.8	2.445	0.0838

σ~K	4	-184.2	380.0	2.674	0.0747

*2 mice removed

Session 9, February 1-5*

	estimate	lcl	ucl
g0	0.024	0.009	0.060
σ	17.8	9.0	35.2

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~bk, *σ*~bk	5	-200.2	412.6	0	0.1991
g0~bk	4	-201.6	412.6	0.049	0.1944
σ~bk	4	-202.2	413.8	1.275	0.1053
null	3	-203.5	413.9	1.362	0.1008
g0~B	4	-202.3	414.0	1.492	0.0945

*5 mice removed

Session 10, March 6-10*

	estimate	lcl	ucl
g0	0.089	0.031	0.232
σ	9.6	9.4	9.8

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k, *σ*~k	5	-342.8	697.1	0	1

*10 mice removed

Session 11, April 1-5*

	estimate	lcl	ucl

g0	0.062	0.033	0.114
σ	9.7	6.8	13.8

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~Bk	4	-370.4	749.6	0	0.2943
σ~Bk	4	-371.3	751.4	1.748	0.1228
g0~bk	4	-371.4	751.5	1.916	0.1129
g0~bk, *σ*~bk	5	-370.5	752.2	2.566	0.0816
null	3	-372.9	752.3	2.681	0.0770

*5 mice removed

Mire 1996-97 (two trapping grids pooled)

Session 1, June 1-5*

	estimate	lcl	ucl
g0	0.198	0.101	0.350
σ	11.3	9.0	14.2

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~b	4	-950.3	1908.9	0	0.4417
σ~b	4	-950.8	1910.0	1.096	0.2554
g0~b, *σ*~b	5	-950.2	1911.0	2.077	0.1564

*7 and 2 mice removed from Grids 1 and 2, respectively

Session 2, July 22-26*

	estimate	lcl	ucl
g0	0.150	0.087	0.246
σ	14.1	11.1	17.9

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~k	4	-822.9	1654.4	0	0.973

*7 mice removed from both Grids 1 and 2

Session 3, September 9-13

	estimate	lcl	ucl
g0	0.053	0.022	0.124
σ	10.3	10.0	10.6

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k, *σ*~k	5	-301.6	615.0	0	1

Session 4, November 19-23

	estimate	lcl	ucl
g0	0.125	0.065	0.225
σ	9.8	9.5	10.1

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k, *σ*~k	5	-228.2	468.9	0	1

Session 5, January 26-30

	estimate	lcl	ucl
g0	0.085	0.038	0.180
σ	18.4	11.6	29.3

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
null	3	-536.9	1080.1	0	0.2463
g0~b	4	-535.8	1080.2	0.118	0.2322
σ~b	4	-536.1	1080.8	0.714	0.1724
g0~B, *σ*~B	5	-535.5	1081.9	1.782	0.1011
g0~B	4	-536.7	1082.0	1.895	0.0955
σ~B	4	-536.9	1082.4	2.255	0.0798
g0~b, *σ*~b	5	-535.8	1082.5	2.439	0.0728

Session 6, March 20-24

	estimate	lcl	ucl
g0	0.050	0.023	0.105
σ	11.2	6.6	19.1

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
null	3	-408.2	822.9	0	0.3036
g0~B	4	-407.8	824.3	1.460	0.1463
σ~b	4	-407.9	824.5	1.650	0.1331
σ~B	4	-408.0	824.7	1.814	0.1226
g0~bk	4	-408.2	825.1	2.252	0.0985
g0~B, *σ*~B	5	-407.0	825.1	2.256	0.0983
σ~bk	4	-408.2	825.1	2.270	0.0976

Mire 1998-99 (two trapping grids pooled)

Session 1, April 11-15*

	estimate	lcl	ucl
g0	0.063	0.043	0.093
σ	9.9	7.7	12.7

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
null	3	-970.5	1947.2	0	1

*1 mouse removed from Grid 1

Session 2, May 11-15*

	estimate	lcl	ucl
g0	0.167	0.101	0.263
σ	6.7	5.2	8.5

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~bk	4	-929.0	1866.2	0	0.5184
g0~Bk	4	-930.4	1869.0	2.803	0.1276
g0~B, *σ*~B	5	-929.5	1869.5	3.249	0.1021
null	3	-931.8	1869.8	3.572	0.0869
g0~B	4	-931.6	1871.5	5.251	0.0375

*11 and 1 mice removed from Grids 1 and 2, respectively

Session 3, June 15-19

	estimate	lcl	ucl
g0	0.28	0.177	0.414

σ	7.6	6.2	9.3

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~k	4	-951.8	1912.1	0	0.6059
g0~k, *σ*~k	5	-951.7	1914.1	1.967	0.2266
σ~K	4	-953.1	1914.7	2.572	0.1675

*2 and 3 mice removed from Grids 1 and 2, respectively

Session 4, July 3-7

	estimate	lcl	ucl
g0	0.615	0.320	0.844
σ	6.7	5.5	8.1

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~k	4	-490.4	989.7	0	0.7170
g0~k *σ*~k	5	-490.2	991.9	2.146	0.2452

Session 5, August 19-23*

	estimate	lcl	ucl
g0	0.793	0.121	0.991
Σ	7.6	6.1	9.5

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k, *σ*~k	5	-446.6	905.0	0	0.7619
σ~k	4	-449.1	907.7	2.399	0.2296

*1 mouse removed from Grid 2

Session 6, September 16-20*

	estimate	lcl	ucl
g0	0.672	0.305	0.906
Σ	8.6	6.9	10.6

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~k	4	-407.0	823.3	0	0.5358
σ~K	4	-408.0	825.3	1.981	0.1990
g0~k, *σ*~k	5	-407.0	826.1	2.754	0.1352

*1 mouse removed from Grid 1

Session 7, October 16-20

	estimate	lcl	ucl
g0	0.374	0.193	0.598
Σ	9.3	7.1	12.2

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~k	4	-392.0	793.2	0	0.6596
g0~k, *σ*~k	5	-392.0	795.8	2.617	0.1782
g0~k	4	-393.9	797.0	3.744	0.1015
g0~B	4	-395.5	800.1	6.883	0.0211

*1 mouse removed from Grid 2

Session 8, November 19-23

	estimate	lcl	ucl
g0	0.441	0.275	0.620
Σ	8.0	6.5	9.8

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~K	4	-500.8	1010.5	0	0.9057
null	3	-505.2	1016.9	6.419	0.0366

Session 9, December 13-17

	estimate	lcl	ucl
g0	0.123	0.060	0.234
Σ	11.2	8.1	15.6

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~K	4	-576.0	1160.6	0	1

Session 10, January 28-February 1*

	estimate	lcl	ucl
g0	0.284	0.142	0.489
Σ	9.5	7.1	12.6

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~b, *σ*~b	5	-784.3	1579.2	0	0.751
σ~b	4	-786.7	1581.8	2.584	0.2063

*2 mice removed from Grid 2

Session 11, March 11-15*

	estimate	lcl	ucl
g0	0.115	0.074	0.176
Σ	7.8	6.2	9.8

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
null	3	-1085.8	2177.8	0	0.2307
g0~Bk	4	-1085.3	2178.9	1.023	0.1383
σ~b	4	-1085.4	2179.0	1.134	0.1308
g0~b	4	-1085.4	2179.0	1.148	0.1299
σ~Bk	4	-1085.4	2179.1	1.240	0.1241

*4 and 2 mice removed from Grids 1 and 2, respectively

Session 12, April 4-8*

	estimate	lcl	ucl
g0	0.121	0.071	0.198
Σ	8.2	6.3	10.6

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~bk	4	-1136.4	2281.1	0	0.2073
null	3	-1137.6	2281.3	0.215	0.1862
g0~B	4	-1136.6	2281.6	0.497	0.1617
g0~b	4	-1137.0	2282.3	1.247	0.1111
g0~b, *σ*~b	5	-1136.1	2282.7	1.600	0.0932

*4 mice removed from Grid 1

Mire, East Grid, 2008-11

Session 1, September 6-10, 2008

	estimate	lcl	ucl
g0	0.285	0.044	0.776
Σ	9.4	6.6	13.3

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~b	4	-164.2	340.0	0	0.526
g0~k	4	-165.6	342.8	2.755	0.1327
σ~k	4	-166.0	343.6	3.597	0.0871
σ~K	4	-166.2	344.1	4.057	0.0692
g0~b, *σ*~b	5	-164.1	344.2	4.189	0.0648

Session 2, November 5-9, 2008

	estimate	lcl	ucl
g0	0.676	0.137	0.965
Σ	13.3	10.8	16.2

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
null	3	-165.9	339.2	0	1.0000

Session 3, January 9-13, 2009

	estimate	lcl	ucl
g0	0.084	0.011	0.425
Σ	10.7	9.0	12.6

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k, *σ*~k	5	-112.1	240.2	0	0.6302
σ~k	4	-114.8	241.2	1.066	0.3698

Session 4, March 7-11, 2009

	estimate	lcl	ucl
g0	0.108	0.037	0.276
Σ	14.2	9.0	22.6

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~B, *σ*~B	5	-209.4	431.2	0	0.5119
g0~b, *σ*~b	5	-209.5	431.4	0.178	0.4683

Session 5, May 10-14, 2009

	estimate	lcl	ucl
g0	0.080	0.044	0.143
Σ	8.6	6.3	11.6

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~B, *σ*~B	5	-802.3	1615.0	0	0.8944
g0~B	4	-805.9	1620.0	4.995	0.0736
g0~b *σ*~b	5	-805.6	1621.7	6.659	0.032

Session 6, June 12-16, 2009

	estimate	lcl	ucl
g0	0.307	0.152	0.521

Σ	7.3	5.4	9.8

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~B, *σ*~B	5	-536.1	1083.2	0	0.7579
g0~K, *σ*~K	5	-538.0	1087.1	3.902	0.1077
g0~B	4	-539.6	1087.8	4.587	0.0765
g0~Bk, *σ*~Bk	5	-538.8	1088.6	5.406	0.0508

Session 7, August 16-20, 2009

	estimate	lcl	ucl
g0	0.566	0.110	0.932
Σ	8.3	5.8	11.9

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~Bk	4	-208.0	425.9	0	0.6269
σ~b	4	-210.0	429.4	3.467	0.1107
null	3	-211.6	430.2	4.313	0.0725
g0~B	4	-210.3	430.5	4.638	0.0617
g0~b, *σ*~b	5	-209.1	431.2	5.347	0.0433

Session 8, October 2-6, 2009

	estimate	lcl	ucl
g0	0.038	0.016	0.086
Σ	10.8	9.5	12.2

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~k	4	-91.4	196.5	0	0.8937
g0~k, *σ*~k	5	-90.4	200.8	4.258	0.1063

Session 9, November 24-28, 2009

	estimate	lcl	ucl
g0	0.149	0.040	0.422
Σ	16.9	8.4	33.7

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~bk	4	-84.5	186.975	0	0.5939
g0~k	4	-84.9	187.801	0.826	0.3929

Session 10, January 18-22, 2010

	estimate	lcl	ucl
g0	0.096	0.033	0.249
Σ	13.3	7.0	25.4

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k, *σ*~k	5	-126.2	267.5	0	0.8763
null	3	-133.3	274.3	6.810	0.0291

Session 11, March 15-19, 2010

	estimate	lcl	ucl
g0	0.213	0.087	0.435
Σ	4.7	3.1	7.0

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~B	4	-375.0	758.6	0	0.5699

g0~B	4	-375.9	760.4	1.783	0.2337
g0~B, *σ*~B	5	-374.8	760.7	2.130	0.1965

Session 12, May 6-10, 2010

	estimate	lcl	ucl
g0	0.078	0.051	0.118
Σ	9.0	7.0	11.6

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~Bk	4	-566.7	1141.1	0	0.4722
σ~Bk	4	-567.2	1142.7	1.624	0.2096
g0~Bk, *σ*~Bk	5	-566.2	1143.0	1.891	0.1834
g0~bk	4	-569.2	1146.7	5.581	0.0290
g0~B, *σ*~B	5	-568.3	1147.2	6.086	0.0225

Session 13, July 6-10, 2010

	estimate	lcl	ucl
g0	0.180	0.081	0.353
Σ	5.2	3.8	7.2

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~K	4	-374.9	758.5	0	0.6395
g0~K, *σ*~K	5	-374.4	760.0	1.454	0.3091
g0~Bk	4	-378.0	764.7	6.122	0.0300

Session 14, August 29-September 2, 2010

	estimate	lcl	ucl
g0	0.172	0.063	0.394
Σ	7.1	4.8	10.6

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k	4	-243.5	496.4	0	0.6285
g0~k, *σ*~k	5	-243.2	498.5	2.073	0.2229
g0~bk	4	-245.5	500.4	3.988	0.0856
σ~k	4	-246.6	502.6	6.190	0.0285
g0~bk, *σ*~bk	5	-245.5	503.2	6.745	0.0216

Session 15, October 25-29, 2010

	estimate	lcl	ucl
g0	0.537	0.124	0.905
Σ	8.3	6.2	11.1

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k	4	-152.7	316.9	0	0.7652
g0~b	4	-154.9	321.4	4.481	0.0814
g0~B	4	-155.0	321.6	4.679	0.0737
g0~bk	4	-155.2	322.0	5.071	0.0606

Session 16, December 19-23, 2010

	estimate	lcl	ucl
g0	0.353	0.079	0.776
Σ	5.1	2.8	9.0

parameters	k	log-likelihood	AICc	ΔAICc	AICwt

σ~k	4	-187.3	384.4	0	0.5091
g0~k	4	-187.7	385.3	0.926	0.3204
g0~k, *σ*~k	5	-186.9	386.7	2.324	0.1593

Session 17, February 12-16, 2011

	estimate	lcl	ucl
g0	0.077	0.013	0.352
Σ	9.1	8.4	10.0

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k, *σ*~k	5	-202.9	417.7	0	0.8345
σ~k	4	-205.8	420.9	3.236	0.1655

Mire, West Grid, 2008-11

Session 1, September 15-19, 2008

	estimate	lcl	ucl
g0	0.114	0.050	0.238
Σ	10.6	9.6	11.7

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~k	4	-150.6	312.6	0	0.7551
g0~k, *σ*~k	5	-149.7	314.8	2.252	0.2449

Session 2, November 16-20, 2008

	estimate	lcl	ucl
g0	0.108	0.027	0.343
Σ	9.8	8.9	10.8

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k, *σ*~k	5	-223.3	458.9	0	0.6940
σ~k	4	-225.5	460.5	1.638	0.3060

Session 3, January 16-20, 2009

	estimate	lcl	ucl
g0	0.225	0.220	0.230
Σ	7.2	7.1	7.3

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~K, *σ*~K	5	-146.7	306.0	0	0.9809

Session 4, March 20-24, 2009

	estimate	lcl	ucl
g0	0.311	0.201	0.447
Σ	4.9	3.8	6.4

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~K	4	-619.5	1247.3	0	1

Session 5, May 18-22, 2009

	estimate	lcl	ucl
g0	0.137	0.078	0.230
Σ	7.5	5.8	9.8

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~B, *σ*~B	5	-630.0	1270.5	0	1

Session 6, July 13-17, 2009

	estimate	lcl	ucl
g0	0.783	0.113	0.990
Σ	4.3	3.4	5.5

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k, *σ*~k	5	-524.1	1059.1	0	1.0000

Session 7, September 8-12, 2009

	estimate	lcl	ucl
g0	0.626	0.190	0.923
Σ	5.4	4.0	7.3

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~k	4	-220.3	450.2	0	0.8597
g0~k	4	-222.2	453.9	3.711	0.1344

Session 8, November 3-6, 2009

	estimate	lcl	ucl
g0	0.333	0.084	0.730
Σ	9.8	6.7	14.4

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~k	4	-152.2	315.2	0	0.4931
g0~k	4	-152.9	316.7	1.522	0.2304
null	3	-155.7	319.0	3.741	0.0760
g0~k, *σ*~k	5	-152.2	319.0	3.757	0.0754
g0~B	4	-154.7	320.3	5.097	0.0386

Session 9, December 28, 2009-January 1, 2010

	estimate	lcl	ucl
g0	0.635	0.013	0.996
Σ	9.9	4.7	21.0

parameters	k	log-likelihood	AICc	ΔAICc	AICwt

null	3	-40.6	87.2	0	1

Session 10, February 22-26, 2010

	estimate	lcl	ucl
g0	0.028	0.027	0.028
Σ	8.7	8.6	8.9

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~K	4	-165.359	339.86	0	1

Session 11, May 16-20, 2010

	estimate	lcl	ucl
g0	0.078	0.037	0.157
Σ	12.7	8.3	19.7

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~bk	4	-363.711	736.047	0	0.3005
σ~b	4	-364.271	737.168	1.121	0.1716
σ~bk	4	-364.383	737.391	1.344	0.1535
null	3	-365.742	737.853	1.806	0.1218
g0~b	4	-365.024	738.673	2.626	0.0808

Session 12, July 20-24, 2010

	estimate	lcl	ucl
g0	0.285	0.115	0.550
Σ	5.0	3.6	7.0

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~K *σ*~K	5	-348.3061	707.703	0	0.9808

Session 13, September 5-9, 2010

	estimate	lcl	ucl
g0	0.745	0.009	0.999
Σ	6.8	5.2	8.9

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~Bk	4	-286.6	582.0	0	0.3805
g0~bk	4	-287.1	583.0	1.034	0.2269
σ~bk	4	-287.1	583.1	1.122	0.2171
g0~bk, *σ*~bk	5	-286.3	584.0	1.976	0.1417
g0~Bk	4	-289.2	587.3	5.312	0.0267

Session 14, October 31 – November 4, 2010

	estimate	lcl	ucl
g0	0.454	0.142	0.807
Σ	6.0	3.5	10.2

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~B	4	-138.5	288.3	0	0.3642
g0~K	4	-138.9	289.1	0.810	0.2429
g0~B	4	-139.4	290.1	1.834	0.1456
null	3	-141.6	291.1	2.810	0.0894
g0~B, *σ*~B	5	-138.4	292.4	4.083	0.0473

Session 15, January 3-7, 2011

	estimate	lcl	ucl
g0	0.112	0.033	0.319
Σ	6.4	3.9	10.5

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~B *σ*~B	5	-175.4	363.4	0	0.3724
σ~K	4	-177.5	364.7	1.248	0.1995
g0~K	4	-177.6	364.9	1.499	0.176
g0~B	4	-178.0	365.5	2.100	0.1303
g0~bk	4	-178.5	366.6	3.215	0.0746

Session 16, February 27-March 3, 2011

	estimate	lcl	ucl
g0	0.108	0.050	0.218
Σ	9.0	9.0	9.1

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~K, *σ*~K	5	-347.3	705.4	0	1

Slope 1991-92

Session 1, May 12-16*

	estimate	lcl	ucl
g0	0.332	0.187	0.516
Σ	7.3	5.9	9.0

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~K, *σ*~K	5	-498.8	1008.4	0	0.5844
σ~K	4	-500.2	1009.1	0.682	0.4156

*42 mice removed

Session 2, June 12-18*

	estimate	lcl	ucl
g0	0.163	0.092	0.273
Σ	11.1	10.6	11.6

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~K, *σ*~K	5	-246.2	504.6	0	0.9927

*4 mice removed, no trapping occurred May14-15 due to weather

Session 3, July 7-11*

	estimate	lcl	ucl
g0	0.082	0.053	0.123
Σ	17.1	13.8	21.0

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~K	4	-411.2	831.4	0	0.6491
g0~K, *σ*~K	5	-410.5	832.6	1.26	0.3457

*3 mice removed, halfnormal detection function used

Session 4, August 16-20

	estimate	lcl	ucl

g0	0.098	0.041	0.214
Σ	12.4	8.3	18.5

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~K	4	-160.2	332.4	0	0.4051
g0~k	4	-160.7	333.4	1.056	0.2389
σ~K	4	-161.2	334.3	1.988	0.1499
σ~k	4	-162.0	336.0	3.646	0.0654
g0~K *σ*~K	5	-160.2	337.0	4.646	0.0397

Session 5, September 8-12*

	estimate	lcl	ucl
g0	0.390	0.156	0.690
Σ	7.6	5.4	10.7

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~Bk	4	-131.6	277.8	0	0.2378
g0~Bk	4	-132.2	279.1	1.305	0.1238
σ~K	4	-132.5	279.8	1.943	0.0900
null	3	-135.2	279.8	2.026	0.0864
g0~bk	4	-132.7	280.0	2.197	0.0793

*2 mice removed

Session 6, October 12-16

	estimate	lcl	ucl
g0	0.355	0.067	0.809
Σ	28.8	16.9	49.0

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k	4	-117.2	255.8	0	0.8435
g0~bk	4	-118.9	259.2	3.369	0.1565

Session 7, November 8-12

	estimate	lcl	ucl
g0	0.385	0.072	0.835
Σ	25.4	15.8	40.9

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~bk	4	-128.2	274.4	0	1

Session 8, December 10-14*

	estimate	lcl	ucl
g0	0.194	0.051	0.519
Σ	25.5	16.6	39.4

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
null	3	-146.0	301.9	0	0.6804
σ~K	4	-144.4	304.9	2.952	0.1555
g0~B	4	-145.5	307.0	5.105	0.053
σ~b	4	-145.8	307.5	5.594	0.0415
g0~b	4	-145.9	307.9	5.939	0.0349

*halfnormal detection function used

Session 9, January 9-12*

	estimate	lcl	ucl

g0	0.998	0.000	1.000
Σ	28.5	19.1	42.7

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
null	3	-96.0	206.1	0	0.9407

* halfnormal detection function used

Session 10, February 12-16

	estimate	lcl	ucl
g0	0.638	0.010	0.997
Σ	12.5	9.0	17.5

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~bk	4	-145.2	301.4	0	0.5415
null	3	-147.8	303.3	1.916	0.2078
σ~K	4	-146.7	304.4	2.964	0.1230
σ~k	4	-147.3	305.6	4.186	0.0668
g0~K	4	-147.6	306.2	4.777	0.0497

Session 11, March 5-9

	estimate	lcl	ucl
g0	0.066	0.023	0.176
Σ	10.2	7.2	14.4

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~k	4	-325.7	660.6	0	0.564
g0~k, *σ*~k	5	-325.6	663.1	2.547	0.1578
g0~B	4	-327.0	663.2	2.624	0.1519

g0~k	4	-327.6	664.4	3.810	0.0839
1 *g0*~B, *σ*~B	5	-326.9	665.8	5.176	0.0424

Slope 1993-94

Session 1, May 8-12*

	estimate	lcl	ucl
g0	0.053	0.034	0.081
Σ	16.3	12.8	20.8

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~bk	4	-627.5	1263.5	0	0.4942
σ~bk	4	-628.4	1265.3	1.857	0.1953
g0~bk, *σ*~bk	5	-627.5	1265.6	2.180	0.1662
σ~B	4	-630.0	1268.4	4.978	0.0410
g0~B, *σ*~B	5	-629.4	1269.5	6.002	0.0246

*4 mice removed

Session 2, June 12-16*

	estimate	lcl	ucl
g0	0.102	0.052	0.191
Σ	16.8	12.5	22.5

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~b	4	-574.9	1158.3	0	0.5907
g0~b, *σ*~b	5	-574.9	1160.6	2.253	0.1915
σ~b	4	-576.3	1161.1	2.768	0.1480
null	3	-579.5	1165.3	6.959	0.0182

*7 mice removed

Session 3, July 16-20

	estimate	lcl	ucl
g0	0.050	0.028	0.087
Σ	13.0	9.8	17.2

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~B	4	-556.3	1121.2	0	0.5588
g0~B, *σ*~B	5	-556.3	1123.5	2.279	0.1788
σ~B	4	-557.7	1124.0	2.767	0.1401
g0~bk	4	-558.7	1126.1	4.849	0.0495
σ~bk	4	-558.8	1126.3	5.025	0.0453

*9 mice removed

Session 4, August 9-13*

	estimate	lcl	ucl
g0	0.113	0.042	0.267
Σ	16.2	12.1	21.7

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~b	4	-456.6	921.9	0	0.4106
g0~b, *σ*~b	5	-455.7	922.6	0.662	0.2949
g0~B, *σ*~B	5	-456.0	923.1	1.172	0.2285
g0~bk	4	-459.5	927.7	5.748	0.0232

*2 mice removed

Session 5, September 11-15*

	estimate	lcl	ucl
g0	0.135	0.071	0.240
Σ	8.5	6.2	11.7

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~bk	4	-393.1	795.2	0	0.2944
g0~bk, *σ*~bk	5	-392.5	796.5	1.304	0.1534
null	3	-395.0	796.5	1.351	0.1498
g0~B	4	-394.6	798.1	2.907	0.0688
σ~B	4	-394.8	798.4	3.249	0.0580

*1 mouse removed

Session 6, October 10-14*

	estimate	lcl	ucl
g0	0.102	0.055	0.182
Σ	9.9	9.7	10.2

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k, *σ*~k	5	-277.4	566.7	0	0.9761

*5 mice removed

Session 7, November 9-13*

	estimate	lcl	ucl
g0	0.169	0.105	0.262
Σ	9.2	9.0	9.4

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k, *σ*~k	5	-269.2	550.8	0	0.9761

*3 mice removed

Session 8, December 9-13*

	estimate	lcl	ucl
g0	0.150	0.134	0.167
Σ	10.0	9.4	10.7

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k, *σ*~k	5	-305.4	623.2	0	0.9608
σ~k	4	-310.0	629.4	6.4	0.0392

*4 mice removed

Session 9, January 11-15*

	estimate	lcl	ucl
g0	0.218	0.112	0.379
Σ	10.3	7.4	14.4

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~k	4	-233.6	477.9	0	0.6755
g0~k	4	-235.1	480.8	2.850	0.1625
g0~k, *σ*~k	5	-233.6	481.5	3.554	0.1143
σ~K	4	-237.1	484.9	6.908	0.0214

*2 mice removed

Session 10, February 10-14*

	estimate	lcl	ucl
g0	0.092	0.052	0.159
Σ	9.8	9.7	9.9

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k, *σ*~k	5	-372.4	755.9	0	1

*21 mice removed

Session 11, March 18-22*

	estimate	lcl	ucl
g0	0.080	0.044	0.143
Σ	14.5	11.3	18.6

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~b, *σ*~b	5	-426.0	863.1	0	0.1392
g0~B	4	-427.2	863.1	0.022	0.1377
null	3	-428.4	863.3	0.173	0.1277
g0~bk	4	-427.4	863.5	0.460	0.1106
σ~bk	4	-427.5	863.8	0.760	0.0952

*7 mice removed

Session 12, April 9-13*

	estimate	lcl	ucl
g0	0.187	0.112	0.294
Σ	11.7	9.3	14.7

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~b	4	-679.3	1367.1	0	0.5349
g0~b, *σ*~b	5	-678.4	1367.5	0.442	0.4288

*10 mice removed

Slope 1998-99 (three trapping grids pooled)

Session 1, April 20-24*

	estimate	lcl	ucl
g0	0.109	0.061	0.189
Σ	10.9	8.7	13.6

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
null	3	-1145.5	2297.1	0	0.2702
g0~b	4	-1144.8	2297.8	0.701	0.1903
g0~B	4	-1145.1	2298.4	1.357	0.1371
g0~b, *σ*~b	5	-1144.0	2298.5	1.402	0.1340
σ~B	4	-1145.3	2298.8	1.750	0.1126
σ~b	4	-1145.4	2299.0	1.911	0.1039

*2 mice removed from Grid 3

Session 2, May 25-29*

	estimate	lcl	ucl
g0	0.388	0.286	0.501
Σ	6.8	5.8	8.0

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~k	4	-1167.3	2342.8	0	0.8313
σ~K	4	-1169.2	2346.7	3.855	0.1210
g0~K, *σ*~K	5	-1169.0	2348.6	5.715	0.0477

*10, 16, and 11 mice removed from Grids 1, 2, and 3, respectively

Session 3, June 28-July 2*

	estimate	lcl	ucl
g0	0.521	0.383	0.656
Σ	8.3	7.2	9.6

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~K	4	-918.7	1846.0	0	0.7700
σ~k	4	-919.9	1848.4	2.417	0.2300

*1, 2, and 2 mice removed from Grids 1, 2, and 3, respectively

Session 4, August 2-6*

	estimate	lcl	ucl
g0	0.303	0.102	0.626
Σ	17.8	14.0	22.7

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~B	4	-611.9	1232.7	0	0.3861
g0~B, *σ*~B	5	-611.2	1233.8	1.11	0.2216
g0~b	4	-612.5	1234.0	1.355	0.1961
g0~b, *σ*~b	5	-612.1	1235.7	3.053	0.0839
σ~k	4	-613.6	1236.2	3.523	0.0663

*halfnormal detection function used

Session 5, August 31-September 4*

	estimate	lcl	ucl
g0	0.554	0.322	0.765
Σ	8.0	7.9	8.1

parameters	k	log-likelihood	AICc	ΔAICc	AICwt

g0~k, *σ*~k	5	-375.1	762.1	0	0.9852

*1, 2, and 2 mice removed from Grids 1, 2, and 3, respectively

Session 6, September 28-October 2

	estimate	lcl	ucl
g0	0.489	0.100	0.892
Σ	9.0	6.2	13.1

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~b	4	-297.7	605.6	0	0.3983
σ~B	4	-298.3	606.9	1.246	0.2136
σ~b	4	-298.6	607.5	1.867	0.1566
g0~B	4	-299.1	608.4	2.812	0.0976
g0~b, *σ*~b	5	-297.7	608.9	3.249	0.0785

Session 7, October 30-November 3

	estimate	lcl	ucl
g0	0.421	0.062	0.890
Σ	9.9	7.3	13.4

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~b	4	-311.7	633.6	0	0.5162
g0~B	4	-312.9	636.0	2.378	0.1572
σ~b	4	-313.1	636.3	2.708	0.1333
g0~b, *σ*~b	5	-311.7	636.7	3.091	0.1101
σ~B	4	-314.3	638.8	5.168	0.039

Session 8, December 9-13

	estimate	lcl	ucl
g0	0.488	0.158	0.829
Σ	11.2	8.6	14.4

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k, *σ*~k	5	-336.0	684.3	0	1

Session 9, January 10-14

	estimate	lcl	ucl
g0	0.195	0.078	0.411
Σ	11.0	7.8	15.5

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~B	4	-368.4	746.1	0	0.6113
g0~B, *σ*~B	5	-368.3	748.6	2.543	0.1714
σ~B	4	-370.4	750.2	4.101	0.0787
g0~b	4	-370.4	750.2	4.136	0.0773
g0~b, *σ*~b	5	-369.8	751.7	5.614	0.0369

Session 10, February 14-18

	estimate	lcl	ucl
g0	0.564	0.272	0.818
Σ	9.4	7.7	11.3

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~k	4	-771.3	1551.1	0	0.5113

g0~k, *σ*~k	5	-770.4	1551.8	0.659	0.3678
σ~K	4	-773.2	1554.9	3.852	0.0745
g0~K, *σ*~K	5	-772.7	1556.3	5.213	0.0377

Session 11, March 25-29

	estimate	lcl	ucl
g0	0.328	0.231	0.442
Σ	9.5	9.3	9.7

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~K, *σ*~K	5	-808.4	1627.6	0	1

Session 12, April 11-15*

	estimate	lcl	ucl
g0	0.180	0.088	0.333
Σ	13.5	10.6	17.1

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~b, *σ*~b	5	-1099.9	2210.2	0	0.7575
σ~b	4	-1102.4	2213.1	2.876	0.1798
g0~B, *σ*~B	5	-1102.5	2215.5	5.301	0.0535

*1 mouse removed from Grid 3

Slope 2008-2011

Session 1, August 30-September 3, 2008

	estimate	lcl	ucl
g0	0.090	0.088	0.091
Σ	8.8	8.6	9.0

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~k	4	-185.7	381.2	0	1

Session 2, October 29-November 2, 2008

	estimate	lcl	ucl
g0	0.740	0.120	0.983
Σ	10.0	7.3	13.8

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~bk	4	-151.8	316.6	0	0.5438
g0~k	4	-152.0	316.9	0.351	0.4562

Session 3, December 26-30, 2008

	estimate	lcl	ucl
g0	0.352	0.093	0.742
Σ	8.6	5.0	14.9

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
null	3	-69.6855	151.4	0	0.8404

Session 4, February 20-24, 2009

	estimate	lcl	ucl
g0	0.072	0.021	0.222
Σ	10.6	9.4	12.0

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k, *σ*~k	5	-174.3	361.5	0	0.7918
σ~k	4	-177.2	364.2	2.672	0.2082

Session 5, April 1-5, 2009

	estimate	lcl	ucl
g0	0.292	0.211	0.389
Σ	8.8	7.5	10.3

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~Bk, *σ*~Bk	5	-774.8	1560.1	0	0.9572

Session 6, June 1-5, 2009

	estimate	lcl	ucl
g0	0.487	0.253	0.728
Σ	7.6	5.1	11.4

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~k	4	-662.8	1334.0	0	0.6574
g0~bk	4	-663.8	1336.0	2.004	0.2414
g0~bk, *σ*~bk	5	-663.5	1337.8	3.743	0.1012

Session 7, August 1-5, 2009

	estimate	lcl	ucl
g0	0.377	0.091	0.786
Σ	9.5	6.3	14.5

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~bk	4	-159.2	329.8	0	0.3985
σ~bk	4	-159.9	331.1	1.345	0.2034
g0~bk, *σ*~bk	5	-158.3	332.1	2.304	0.1259
g0~Bk	4	-160.5	332.3	2.545	0.1116
σ~Bk	4	-160.6	332.6	2.861	0.0953

Session 8, October 1-5, 2009

	estimate	lcl	ucl
g0	0.084	0.048	0.142
Σ	10.1	9.5	10.7

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~k	4	-79.33613	176.672	0	0.9897

Session 9, November 24-28, 2009*

	estimate	lcl	ucl
g0	0.084	0.031	0.209
Σ	12.6	7.0	22.6

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
null	3	-64.4	142.8	0	1

*halfnormal detection function used

Session 10, January 18-22, 2010

	estimate	lcl	ucl
g0	0.160	0.052	0.398
Σ	10.5	5.7	19.4

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
null	3	-92.9	196.7	0	0.7932
g0~B	4	-91.7	201.4	4.694	0.0759
σ~B	4	-91.7	201.5	4.789	0.0724
σ~k	4	-92.5	202.9	6.282	0.0343
g0~k	4	-92.8	203.6	6.972	0.0243

Session 11, March 15-19, 2010

	estimate	lcl	ucl
g0	0.340	0.129	0.641
Σ	8.1	6.4	10.4

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k	4	-301.7	612.7	0	0.4676
σ~k	4	-302.0	613.3	0.565	0.3525
g0~k, *σ*~k	5	-301.3	614.6	1.910	0.1799

Session 12, May 1-5, 2010

	estimate	lcl	ucl
g0	0.109	0.071	0.163
Σ	7.8	6.2	9.8

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~Bk	4	-587.0	1182.3	0	0.317
σ~Bk	4	-587.4	1183.1	0.784	0.2142
g0~Bk, *σ*~Bk	5	-586.6	1183.6	1.330	0.163
g0~bk	4	-588.3	1184.8	2.531	0.0894
null	3	-589.3	1184.9	2.557	0.0883

Session 13, July 6-10, 2010

	estimate	lcl	ucl
g0	0.030	0.011	0.077
Σ	22.2	11.8	41.7

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k, *σ*~k	5	-195.0	402.3	0	0.573
g0~K, *σ*~K	5	-195.5	403.3	0.994	0.3486
σ~K	4	-198.5	406.5	4.199	0.0702

Session 14, August 20-24, 2010

	estimate	lcl	ucl
g0	0.358	0.175	0.594
Σ	8.7	8.6	8.9

parameters	k	log-likelihood	AICc	ΔAICc	AICwt

g0~k, *σ*~k	5	-169.3	352.1	0	0.9737

Session 15, October 15-19, 2010

	estimate	lcl	ucl
g0	0.043	0.041	0.045
Σ	8.9	8.5	9.3

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k, *σ*~k	5	-72.2	163.0	0	1

Session 16, December 12-16, 2010

	estimate	lcl	ucl
g0	0.120	0.009	0.678
Σ	8.5	2.9	25.1

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~Bk	4	-54.5	130.3	0	0.4505
σ~Bk	4	-55.0	131.3	0.980	0.2760
g0~bk	4	-55.7	132.7	2.412	0.1349
g0~k	4	-56.2	133.6	3.370	0.0835
null	3	-61.2	134.5	4.204	0.0551

Session 17, February 5-9, 2011

	estimate	lcl	ucl
g0	0.208	0.056	0.539
Σ	5.0	3.2	7.8

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
null	3	-167.7	342.3	0	0.3070
g0~bk	4	-166.7	342.9	0.651	0.2217
σ~B	4	-167.2	344.0	1.720	0.1299
g0~b	4	-167.3	344.1	1.891	0.1193
g0~B	4	-167.4	344.4	2.124	0.1062

Biotic 1991-92

Session 1, May 19-23*

	estimate	lcl	ucl
g0	0.317	0.197	0.468
σ	5.5	4.3	7.0

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~B	4	-609.9	1228.1	0	0.2308
g0~bk	4	-610.2	1228.6	0.549	0.1754
σ~bk	4	-610.2	1228.7	0.609	0.1702
null	3	-611.6	1229.4	1.318	0.1194
g0~bk, *σ*~bk	5	-610.2	1230.8	2.684	0.0603

*63 mice removed

Session 2, June 23-27*

	estimate	lcl	ucl
g0	0.166	0.091	0.283
σ	9.3	7.4	11.7

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~K, *σ*~K	5	-698.0	1406.8	0	0.2463
g0~K	4	-699.6	1407.6	0.806	0.1646
g0~k, *σ*~k	5	-698.5	1407.8	1.010	0.1486
σ~b	4	-700.2	1408.8	2.032	0.0892
σ~k	4	-700.5	1409.5	2.702	0.0638

*10 mice removed

Session 3, July 14-19*

	estimate	lcl	ucl
g0	0.238	0.146	0.362
σ	8.3	6.8	10.4

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~k	4	-529.3	1067.5	0	0.328
g0~k	4	-529.5	1067.9	0.409	0.2673
g0~k, *σ*~k	5	-529.0	1069.2	1.682	0.1414
σ~bk	4	-530.7	1070.2	2.680	0.0859
g0~bk	4	-531.6	1071.9	4.458	0.0353

*3 mice removed, July 15th not trapped due to weather

Session 4, August 23-27*

	estimate	lcl	ucl
g0	0.227	0.137	0.353
σ	9.1	7.3	11.4

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~K, *σ*~K	5	-488.1	987.6	0.000	0.3835
σ~k	4	-489.6	988.2	0.586	0.2861
g0~K	4	-490.0	989.0	1.396	0.1908
g0~k, *σ*~k	5	-489.6	990.6	3.072	0.0825
g0~k	4	-491.2	991.4	3.812	0.0570

*1 mouse removed

Session 5, September 17-21*

	estimate	lcl	ucl

g0	0.449	0.287	0.623
σ	7.5	6.3	8.9

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~k	4	-549.6	1108.1	0	0.7170
g0~k, *σ*~k	5	-549.6	1110.5	2.349	0.2215
g0~k	4	-552.1	1113.0	4.913	0.0615

*2 mice removed

Session 6, October 21-25

	estimate	lcl	ucl
g0	0.225	0.120	0.383
σ	6.5	4.9	8.5

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~B	4	-460.2	929.2	0	0.1993
g0~b	4	-460.4	929.7	0.501	0.1551
g0~bk, *σ*~bk	5	-459.2	929.7	0.535	0.1525
g0~bk	4	-460.5	929.9	0.766	0.1359
g0~B, *σ*~B	5	-459.5	930.3	1.150	0.1121

Session 7, November 16-21*

	estimate	lcl	ucl
g0	0.306	0.198	0.441
σ	9.2	7.5	11.2

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~Bk	4	-506.2	1021.5	0	0.3707

σ~bk	4	-506.9	1022.9	1.373	0.1866
g0~bk	4	-507.0	1023.2	1.654	0.1621
σ~Bk	4	-507.6	1024.3	2.777	0.0925
g0~K	4	-507.6	1024.4	2.873	0.0881

*November 18 not trapped due to weather

Session 8, December 17-22*

	estimate	lcl	ucl
g0	0.117	0.083	0.162
σ	8.8	8.7	8.9

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~K, *σ*~K	5	-607.2	1225.2	0	1.0000

*December 19 not trapped due to weather

Session 9, January 16-21*

	estimate	lcl	ucl
g0	0.212	0.116	0.357
σ	11.2	9.0	13.8

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~b, *σ*~b	5	-693.1	1396.9	0	0.9278
σ~b	4	-697.0	1402.5	5.623	0.0558

*January 18 not trapped due to weather

Session 10, February 18-22

	estimate	lcl	ucl
g0	0.158	0.104	0.233
σ	6.9	4.9	9.8

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~bk	4	-769.9738	1548.3	0	0.4501
σ~k	4	-770.5201	1549.4	1.092	0.2607
g0~bk, *σ*~bk	5	-769.9151	1550.4	2.088	0.1584
σ~bk	4	-771.4019	1551.2	2.856	0.1079

Session 11, March 14-19*

	estimate	lcl	ucl
g0	0.130	0.129	0.132
σ	9.0	8.9	9.1

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~K, *σ*~K	5	-919.5	1849.5	0	1

*1 mouse removed, March 17 not trapped due to weather

Biotic 1993-94

Session 1, May 13-17*

	estimate	lcl	ucl
g0	0.173	0.098	0.287
σ	8.6	6.2	12.0

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~b	4	-612.2	1232.8	0	0.4174
g0~b	4	-612.3	1232.9	0.055	0.4060
g0~b, *σ*~b	5	-612.0	1234.6	1.762	0.1729

*21 mice removed

Session 2, June 19-23*

	estimate	lcl	ucl
g0	0.064	0.041	0.100
σ	9.5	9.4	9.6

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~K, *σ*~K	5	-624.456	1259.5	0	1.0000

*7 mice removed

Session 3, July 23-25*

	estimate	lcl	ucl
g0	0.140	0.015	0.633
σ	7.0	2.5	19.9

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~B, *σ*~B	5	-349.2	709.2	0	0.3850
g0~b, *σ*~b	5	-350.0	710.9	1.677	0.1665
g0~Bk	4	-351.9	712.2	3.022	0.0850
g0~B	4	-351.9	712.3	3.040	0.0842
null	3	-353.0	712.3	3.074	0.0828

*9 mice removed

Session 4, August 23-27*

	estimate	lcl	ucl
g0	0.053	0.024	0.111
σ	9.3	9.1	9.4

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~K, *σ*~K	5	-473.2	957.3	0	1

*4 mice removed

Session 5, September 26-30*

	estimate	lcl	ucl
g0	0.256	0.137	0.427
σ	8.1	6.0	11.0

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~b	4	-486.5	981.6	0	0.6029
g0~b, *σ*~b	5	-486.4	983.6	2.064	0.2148
σ~b	4	-487.7	983.9	2.393	0.1822

*9 mice removed

Session 6, October 15-19*

	estimate	lcl	ucl
g0	0.386	0.186	0.633
σ	6.5	5.1	8.2

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k, *σ*~k	5	-626.6	1264.1	0	0.5053
σ~k	4	-628.4	1265.4	1.370	0.2547
σ~K	4	-628.9	1266.4	2.309	0.1593
g0~K, *σ*~K	5	-628.5	1267.9	3.797	0.0757

*23 mice removed

Session 7, November 15-19*

	estimate	lcl	ucl
g0	0.286	0.140	0.498
σ	6.0	4.6	7.8

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~k	4	-424.4	857.5	0	0.5818
g0~k, *σ*~k	5	-423.9	859.0	1.485	0.2769
g0~k	4	-426.3	861.3	3.871	0.0840

*22 mice removed

Session 8, December 27-31*

	estimate	lcl	ucl
g0	0.069	0.035	0.131

σ	9.8	9.7	10.0

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k, *σ*~k	5	-358.5	728.0	0	1.0000

*18 mice removed

Session 9, January 17-21*

	estimate	lcl	ucl
g0	0.079	0.045	0.136
σ	15.6	12.0	20.3

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~b, *σ*~b	5	-580.8	1172.3	0	0.9876

*11 mice removed

Session 10, February 19-23*

	estimate	lcl	ucl
g0	0.193	0.122	0.291
σ	5.4	4.3	6.9

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~b	4	-610.9	1230.1	0	0.1583
null	3	-612.0	1230.2	0.035	0.1555
σ~Bk	4	-611.4	1231.2	1.073	0.0925
g0~b, *σ*~b	5	-610.4	1231.3	1.151	0.0890
σ~B	4	-611.5	1231.3	1.211	0.0864

*23 mice removed

Session 11, March 25-29*

	estimate	lcl	ucl
g0	0.248	0.146	0.389
σ	5.2	4.3	6.3

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~bk	4	-654.8	1318.0	0	0.1361
g0~b	4	-654.9	1318.1	0.094	0.1299
null	3	-655.9	1318.1	0.116	0.1284
g0~bk	4	-655.3	1318.9	0.910	0.0864
g0~bk, *σ*~bk	5	-654.2	1318.9	0.946	0.0848

*45 mice removed

Session 12, April 18-22*

	estimate	lcl	ucl
g0	0.121	0.065	0.214
σ	7.1	4.9	10.2

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~b	4	-597.1	1202.5	0	0.4263
g0~b, *σ*~b	5	-596.2	1202.9	0.394	0.3501
g0~b	4	-599.5	1207.2	4.709	0.0405
σ~B	4	-599.5	1207.3	4.873	0.0373
null	3	-600.6	1207.4	4.926	0.0363

*12 mice removed

Biotic 1996-97 (two trapping grids pooled)

Session 1, May 4-8*

	estimate	lcl	ucl
g0	0.200	0.155	0.253
σ	7.8	6.9	9.0

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~bk, *σ*~bk	5	-1801.3	3612.8	0	0.4921
g0~bk	4	-1802.4	3612.9	0.073	0.4745
σ~bk	4	-1805.0	3618.2	5.379	0.0334

*12 and 4 mice removed from Grids 1 and 2, respectively

Session 2, July 15-19*

	estimate	lcl	ucl
g0	0.130	0.092	0.181
σ	9.6	9.4	9.7

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~K, *σ*~K	5	-925.3	1861.3	0	1

*5 and 6 mice removed from Grids 1 and 2, respectively

Session 3, September 2-6*

	estimate	lcl	ucl
g0	0.665	0.387	0.862
σ	4.7	4.6	4.8

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k, *σ*~k	5	-471.4	953.9	0	1

*4 mice removed from Grid 1

Session 4, November 5-9

	estimate	lcl	ucl
g0	0.044	0.018	0.103
σ	11.1	10.8	11.5

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k, *σ*~k	5	-349.9	711.3	0	1

Session 5, January 21-25

	estimate	lcl	ucl
g0	0.096	0.047	0.188
σ	18.8	12.8	27.6

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~b, *σ*~b	5	-576.4	1163.5	0	0.5585
σ~b	4	-577.7	1164.0	0.497	0.4356

Session 6, March 12-16

	estimate	lcl	ucl
g0	0.063	0.030	0.126
σ	11.0	8.0	15.1

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~bk	4	-768.1	1544.5	0	0.4653
g0~bk, *σ*~bk	5	-767.8	1546.1	1.597	0.2094
σ~bk	4	-769.1	1546.6	2.092	0.1635
g0~b	4	-770.2	1548.7	4.254	0.0555
σ~b	4	-770.4	1549.1	4.598	0.0467

Session 7, April 27-May 1

	estimate	lcl	ucl
g0	0.107	0.071	0.159
σ	11.2	8.3	15.1

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~b, *σ*~b	5	-1414.6	2839.6	0	0.2603
σ~b	4	-1416.0	2840.3	0.677	0.1855
null	3	-1417.3	2840.7	1.109	0.1495
g0~B, *σ*~B	5	-1415.4	2841.1	1.526	0.1214
σ~B	4	-1416.5	2841.2	1.605	0.1167

Biotic 1998-99 (three trapping grids pooled)

Session 1, April 11-15

	estimate	lcl	ucl
g0	0.038	0.020	0.069
σ	13.2	9.7	18.0

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~B	4	-1494.5	2997.2	0	0.4418
g0~B, *σ*~B	5	-1494.1	2998.5	1.297	0.231
g0~b	4	-1495.5	2999.2	1.942	0.1673
σ~B	4	-1495.7	2999.5	2.291	0.1405
σ~b	4	-1497.9	3004.0	6.825	0.0146

Session 2, May 18-22*

	estimate	lcl	ucl
g0	0.346	0.222	0.495
σ	4.5	3.8	5.4

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~K	4	-1279.6	2567.4	0	0.7276
g0~K, *σ*~K	5	-1279.6	2569.6	2.144	0.2491
g0~K	4	-1283.0	2574.3	6.878	0.0234

*3, 5, and 2 mice removed from Grids 1, 2 and 3, respectively

Session 3, June 22-26*

	estimate	lcl	ucl

g0	0.388	0.141	0.711
σ	4.7	3.7	5.9

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k, *σ*~k	5	-1254.7	2519.9	0	1

*2, 1, and 6 mice removed from Grids 1, 2 and 3, respectively

Session 4, July 20-23*

	estimate	lcl	ucl
g0	0.732	0.432	0.907
σ	6.6	5.6	7.7

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~k	4	-924.3	1857.1	0	0.6454
g0~K	4	-925.5	1859.4	2.3	0.2044
σ~K	4	-925.8	1860.0	2.915	0.1503

*3, 4, and 1 mice removed from Grids 1, 2 and 3, respectively

Session 5, August 26-30*

	estimate	lcl	ucl
g0	0.370	0.163	0.640
σ	7.5	6.1	9.1

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~B	4	-628.1	1265.1	0	0.3993
g0~b	4	-628.5	1265.9	0.868	0.2587
g0~B, *σ*~B	5	-628.1	1267.5	2.443	0.1177
g0~b, *σ*~b	5	-628.3	1267.8	2.742	0.1014

σ~k	4	-629.6	1268.1	3.071	0.0860

*1 mouse removed from Grid 1

Session 6, September 1-5

	estimate	lcl	ucl
g0	0.660	0.351	0.874
σ	8.5	7.0	10.4

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~Bk	4	-528.3	1065.6	0	0.3253
g0~Bk	4	-528.6	1066.2	0.637	0.2366
null	3	-530.2	1067.1	1.490	0.1544
g0~B	4	-529.8	1068.7	3.110	0.0701
σ~B	4	-529.8	1068.7	3.122	0.0697

Session 7, October 23-27

	estimate	lcl	ucl
g0	0.470	0.289	0.659
σ	7.8	6.4	9.5

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~k	4	-543.1	1095.1	0	0.6514
g0~k, *σ*~k	5	-543.0	1097.4	2.304	0.2058
σ~K	4	-545.7	1100.4	5.285	0.0464
g0~K	4	-546.3	1101.6	6.477	0.0255
null	3	-547.7	1101.9	6.824	0.0215

Session 8, November 26-30

	estimate	lcl	ucl
g0	0.213	0.208	0.217
σ	9.3	9.1	9.4

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k, *σ*~k	5	-436.3	883.9	0	1

Session 9, December 22-26*

	estimate	lcl	ucl
g0	0.214	0.132	0.327
σ	7.0	5.4	9.0

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~K	4	-1264.6	2537.4	0	0.6051
g0~K, *σ*~K	5	-1264.2	2538.8	1.366	0.3056
g0~K	4	-1266.5	2541.3	3.826	0.0893

*2 mice removed from both Grids 2 and 3

Session 10, February 5-9*

	estimate	lcl	ucl
g0	0.398	0.209	0.622
σ	5.3	4.4	6.4

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~K, *σ*~K	5	-1675.5	3361.4	0	0.6762
σ~K	4	-1677.3	3362.8	1.473	0.3238

*2, 2, and 7 mice removed from Grids 1, 2 and 3, respectively

Session 11, March 19-23*

	estimate	lcl	ucl
g0	0.248	0.162	0.362
σ	6.7	5.5	8.0

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~bk	4	-1890.2	3788.6	0	0.824
g0~b, *σ*~b	5	-1891.0	3792.2	3.605	0.1359
g0~b	4	-1893.4	3795.0	6.412	0.0334

*3, 1, and 3 mice removed from Grids 1, 2 and 3, respectively

Session 12, April 10-14*

	estimate	lcl	ucl
g0	0.197	0.125	0.296
σ	9.3	7.5	11.5

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~b, *σ*~b	5	-1954.4	3919.0	0	0.7259
g0~bk	4	-1956.5	3921.1	2.07	0.2579

*2 mice removed from Grid 1

Biotic East Grid 2008-11

Session 1, August 22-26, 2008

	estimate	lcl	ucl
g0	0.399	0.202	0.636
σ	3.6	2.5	5.1

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~k	4	-371.1	751.0	0	0.9679
g0~K	4	-374.5	757.841	6.815	0.0321

Session 2, October 22-26, 2008

	estimate	lcl	ucl
g0	0.461	0.164	0.790
σ	5.7	3.9	8.4

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~bk, *σ*~bk	5	-359.2	729.9	0	0.2809
g0~K	4	-360.8	730.5	0.650	0.2030
g0~bk	4	-361.4	731.6	1.784	0.1151
g0~K, *σ*~K	5	-360.3	732.1	2.218	0.0927
σ~k	4	-361.6	732.1	2.251	0.0912

Session 3, January 2-6, 2009

	estimate	lcl	ucl
g0	0.623	0.018	0.993
σ	4.1	3.3	5.3

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~Bk	4	-446.8	902.3	0	0.4188
g0~Bk, *σ*~Bk	5	-446.2	903.3	1.061	0.2464
g0~B	4	-447.5	903.5	1.239	0.2254
g0~B, *σ*~B	5	-447.5	905.8	3.546	0.0711
σ~B	4	-449.9	908.4	6.133	0.0195

Session 4, February 27-March 3, 2009

	estimate	lcl	ucl
g0	0.353	0.167	0.597
σ	5.3	4.1	6.9

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~Bk, *σ*~Bk	5	-456.6	924.1	0	0.4720
σ~Bk	4	-458.4	925.3	1.190	0.2604
g0~Bk	4	-458.8	926.3	2.137	0.1622
g0~bk *σ*~1	4	-460.3	929.3	5.129	0.0363
1 *g0*~K *σ*~K	5	-459.4	929.6	5.475	0.0306

Session 5, April 22-26, 2009

	estimate	lcl	ucl
g0	0.570	0.295	0.807
σ	4.1	3.2	5.1

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~Bk	4	-650.3	1309.0	0	0.5159
g0~Bk, *σ*~Bk	5	-649.4	1309.3	0.378	0.4270

g0~bk	4	-653.1	1314.5	5.532	0.0325
g0~bk, *σ*~bk	5	-652.7	1315.9	6.906	0.0163

Session 6, June 25-29, 2009

	estimate	lcl	ucl
g0	0.275	0.083	0.616
σ	6.0	3.5	10.3

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~bk	4	-199.4	408.1	0	0.3667
σ~Bk	4	-200.1	409.7	1.572	0.1671
g0~Bk	4	-200.4	410.2	2.026	0.1332
g0~bk, *σ*~bk	5	-199.4	410.9	2.795	0.0907
g0~Bk, *σ*~Bk	5	-199.4	411.0	2.911	0.0856

Session 7, August 21-25, 2009

	estimate	lcl	ucl
g0	0.185	0.053	0.482
σ	10.1	6.0	16.9

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
null	3	-147.0	301.2	0	0.2483
g0~Bk	4	-146.1	302.5	1.278	0.1311
σ~Bk	4	-146.1	302.5	1.278	0.1311
σ~bk	4	-146.5	303.4	2.130	0.0856
g0~bk	4	-146.6	303.6	2.340	0.0771

Session 8, October 15-19, 2009

	estimate	lcl	ucl
g0	0.240	0.081	0.531
σ	10.4	5.8	18.7

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
null	3	-96.7	203.4	0	0.5794
σ~B	4	-96.2	208.5	5.093	0.0454
σ~Bk	4	-96.3	208.6	5.252	0.0419
σ~bk	4	-96.3	208.7	5.273	0.0415
g0~B	4	-96.4	208.7	5.347	0.0400

Session 9, December 10-14, 2009

	estimate	lcl	ucl
g0	0.104	0.041	0.241
σ	7.5	4.6	12.3

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~Bk	4	-159.0	327.7	0	0.2111
σ~bk	4	-159.0	327.9	0.162	0.1947
σ~Bk	4	-159.1	328.1	0.320	0.1799
g0~bk	4	-159.2	328.2	0.481	0.1660
null	3	-161.7	330.5	2.749	0.0534

Session 10, February 4-8, 2010

	estimate	lcl	ucl
g0	0.332	0.122	0.640

σ	12.5	7.2	21.7

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~b	4	-304.5	617.7	0	0.6301
g0~b, *σ*~b	5	-303.9	619.0	1.264	0.3349

Session 11, April 1-5, 2010

	estimate	lcl	ucl
g0	0.135	0.079	0.220
σ	8.0	6.1	10.6

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~bk	4	-518.9	1046.2	0	0.5673
g0~bk, *σ*~bk	5	-518.5	1047.7	1.484	0.2701
σ~bk	4	-520.9	1050.3	4.058	0.0746
g0~Bk	4	-521.3	1051.0	4.768	0.0523
g0~Bk, *σ*~Bk	5	-521.7	1053.0	6.842	0.0185

Session 12, June 25-29, 2010

	estimate	lcl	ucl
g0	0.058	0.018	0.169
σ	9.7	6.3	14.9

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~B, *σ*~B	5	-250.2	512.0	0	0.5453
g0~b, *σ*~b	5	-250.5	512.5	0.538	0.4167
g0~B	4	-254.1	517.3	5.323	0.0381

Session 13, August 20-24, 2010

	estimate	lcl	ucl
g0	0.442	0.108	0.839
σ	8.5	5.9	12.3

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~Bk	4	-174.0	358.3	0	0.4016
g0~bk	4	-174.8	359.8	1.469	0.1927
g0~Bk, *σ*~Bk	5	-173.6	360.8	2.460	0.1174
σ~bk	4	-175.5	361.3	2.973	0.0908
g0~bk, *σ*~bk	5	-173.9	361.3	3.039	0.0879

Session 14, October 15-19, 2010

	estimate	lcl	ucl
g0	0.275	0.044	0.757
σ	7.9	4.4	14.2

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
null	3	-94.2	196.9	0	0.4148
g0~B	4	-92.4	197.2	0.313	0.3547
g0~K, *σ*~K	5	-91.1	199.8	2.877	0.0984
σ~B	4	-93.8	200.0	3.098	0.0881
g0~B, *σ*~B	5	-91.9	201.4	4.495	0.0438

Session 15, December 12-16, 2010

	estimate	lcl	ucl

g0	0.184	0.059	0.445
σ	9.4	5.9	15.0

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~bk	4	-145.0	300.6	0	0.5319
σ~bk	4	-146.5	303.6	3.028	0.117
g0~bk, *σ*~bk	5	-144.9	303.8	3.294	0.1025
g0~Bk	4	-147.5	305.4	4.862	0.0468
g0~b, *σ*~b	5	-146.0	306.0	5.473	0.0345

Session 16, February 5-9, 2011

	estimate	lcl	ucl
g0	0.285	0.152	0.469
σ	8.1	5.9	11.1

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~bk	4	-312.2	633.2	0	0.7509
g0~bk, *σ*~bk	5	-312.0	635.4	2.207	0.2491

Biotic West Grid, 2008-011

Session 1, September 15-19, 2008

	estimate	lcl	ucl
g0	0.194	0.081	0.397
σ	6.5	5.1	8.4

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k	4	-343.8	696.5	0	0.6026
g0~k, *σ*~k	5	-343.4	698.2	1.768	0.2490
g0~K	4	-347.0	700.9	4.403	0.0667
σ~k	4	-346.0	701.1	4.614	0.0600
g0~K, *σ*~K	5	-345.8	703.1	6.642	0.0218

Session 2, November 16-20, 2008

	estimate	lcl	ucl
g0	0.124	0.031	0.384
σ	6.0	4.3	8.4

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~B	4	-352.5	713.9	0	0.4866
g0~b, *σ*~b	5	-352.2	715.7	1.791	0.1987
g0~b	4	-353.7	716.2	2.288	0.1550
g0~B, *σ*~B	5	-352.5	716.3	2.388	0.1475

Session 3, January 16-20, 2009

	estimate	lcl	ucl

g0	0.523	0.325	0.713
σ	4.1	3.6	4.8

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~B	4	-505.6	1019.6	0	0.7852
g0~bk	4	-506.9	1022.2	2.662	0.2075

Session 4, March 20-24, 2009

	estimate	lcl	ucl
g0	0.504	0.345	0.663
σ	5.8	4.9	6.8

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~bk, *σ*~bk	5	-924.3	1859.1	0	1

Session 5, May 18-22, 2009

	estimate	lcl	ucl
g0	0.160	0.100	0.247
σ	9.0	6.8	12.0

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~bk	4	-491.1	990.8	0	0.6232
g0~bk, *σ*~bk	5	-490.5	991.8	1.006	0.3768

Session 6, July 13-17, 2009

	estimate	lcl	ucl

g0	0.663	0.229	0.929
σ	4.4	3.3	6.1

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~Bk	4	-360.8	730.2	0	0.5486
g0~Bk, *σ*~Bk	5	-360.0	731.0	0.799	0.3679
g0~bk	4	-363.7	736.0	5.792	0.0303
g0~Bk	4	-363.7	736.1	5.854	0.0294

Session 7, September 8-12, 2009

	estimate	lcl	ucl
g0	0.470	0.047	0.941
σ	8.5	5.2	13.8

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~bk	4	-160.8	332.2	0	0.4988
σ~K	4	-161.7	334.0	1.845	0.1983
g0~bk, *σ*~bk	5	-160.3	334.6	2.431	0.1479
g0~k	4	-163.3	337.1	4.981	0.0413
g0~K	4	-163.3	337.2	5.046	0.0400

Session 8, November 2-6, 2009

	estimate	lcl	ucl
g0	0.019	0.008	0.047
σ	17.2	9.4	31.2

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~k	4	-110.7	232.5	0	0.7891

g0~k, *σ*~k	5	-110.7	236.4	3.889	0.1129
σ~K	4	-112.9	237.0	4.452	0.0852

Session 9, December 28, 2009-January 1, 2010

	estimate	lcl	ucl
g0	0.070	0.042	0.116
σ	14.8	9.7	22.6

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~bk	4	-445.0	898.5	0	0.7431
g0~bk, *σ*~bk	5	-444.9	900.6	2.124	0.2569

Session 10, February 22-26, 2010

	estimate	lcl	ucl
g0	0.338	0.128	0.638
σ	4.2	3.2	5.6

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~bk	4	-502.2	1012.8	0	0.4078
g0~bk, *σ*~bk	5	-501.9	1014.4	1.627	0.1808
g0~Bk	4	-503.2	1014.9	2.053	0.1461
σ~bk	4	-503.5	1015.5	2.643	0.1088
σ~Bk	4	-503.9	1016.2	3.346	0.0765

Session 11, May 16-20, 2010

	estimate	lcl	ucl

g0	0.331	0.148	0.584
σ	4.7	3.5	6.4

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~bk	4	-359.8	728.3	0	0.4550
g0~bk, *σ*~bk	5	-358.7	728.5	0.159	0.4202
g0~bk	4	-361.1	730.9	2.587	0.1248

Session 12, July 20-24, 2010

	estimate	lcl	ucl
g0	0.218	0.108	0.393
σ	8.1	5.3	12.5

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~B	4	-249.0	507.5	0	0.2602
σ~Bk	4	-249.1	507.8	0.301	0.2239
g0~Bk	4	-249.2	507.9	0.401	0.2130
g0~B	4	-250.2	509.9	2.418	0.0777
g0~B, *σ*~B	5	-249.0	510.3	2.856	0.0624

Session 13, September 5-9, 2010

	estimate	lcl	ucl
g0	0.147	0.037	0.432
σ	7.8	3.5	17.5

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~B	4	-197.5	404.5	0	0.3472
g0~b, *σ*~b	5	-196.2	404.7	0.177	0.3178

g0~B, *σ*~B	5	-196.7	405.7	1.215	0.1891
σ~B	4	-199.8	409.0	4.519	0.0362
g0~k	4	-200.5	410.5	6.023	0.0171

Session 14, October 31-November 4, 2010

	estimate	lcl	ucl
g0	0.661	0.152	0.955
σ	7.3	7.1	7.4

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~K, *σ*~K	5	-88.4	193.5	0	1

Session 15, January 3-6, 2011

	estimate	lcl	ucl
g0	0.183	0.051	0.481
σ	5.4	4.0	7.3

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
g0~k	4	-274.0	556.8	0	0.6601
g0~k, *σ*~k	5	-273.7	558.7	1.863	0.2601
σ~k	4	-276.7	562.2	5.431	0.0437

Session 16, February 27-March 3, 2011

	estimate	lcl	ucl
g0	0.522	0.286	0.749
σ	4.8	3.9	5.9

parameters	k	log-likelihood	AICc	ΔAICc	AICwt
σ~bk	4	-665.9	1340.2	0	0.6157
g0~bk, *σ*~bk	5	-665.9	1342.3	2.089	0.2166
g0~bk	4	-667.6	1343.5	3.313	0.1175
g0~Bk, *σ*~Bk	5	-667.8	1346.3	6.046	0.0300
σ~Bk	4	-669.3	1347.1	6.834	0.0202

Appendix D: R Code for sheathbill whole-island population growth rate and confidence intervals (Chapter 3)

```
# Sheathbill Females
#-------------------------------------------------------------------------
fsa1 <-  0.979 # breeding adult survival season 1
fsa2 <-  0.962  # breeding adult survival season 2
fsf1 <-  0.671 # fledgling survival season 1
fsf2 <-  0.602   # fledgling survival season 2
fs11 <-  0.880   # one-year olds survival season 1
fs12 <-  0.868 # one-year olds survival season 2
fs21 <-  0.880  # two-year olds survival season 1
fs22 <-  0.868  # two-year olds survival season 2

# Sheathbill Males
#-------------------------------------------------------------------------
msa1 <-  0.979 # breeding adult survival season 1
msa2 <-  0.962  # breeding adult survival season 2
msf1 <-  0.671 # fledgling survival season 1
msf2 <-  0.602   # fledgling survival season 2
ms11 <-  0.880   # one-year olds survival season 1
ms12 <-  0.868 # one-year olds survival season 2
ms21 <-  0.880  # two-year olds survival season 1
ms22 <-  0.868  # two-year olds survival season 2

# Reproduction
ffled <- 0.34   # number of females produced by each sex
mfled <- 0.12   # number of males produced by each sex
mbp <- 0.793 #male breeding probability


# simulation to estimate population growth rate when sex ratio not fixed: limited by rarer
sex
# ************************************************************************
ts.length<-502  #set desired length of time series
r<-rep(NA,ts.length-1)
density<-rep(1/6,6)  #adds starting values for population vector
N<-sum(density)

for (i in 1:(ts.length-1)) {
  fdf<-(ffled*min(c(sum(density[1:3]),sum(density[4:6]))))*(fsf1*fsf2)  #daughters produced
by females
  fdm<-(ffled*min(c(sum(density[1:3]),sum(density[4:6]))))*(fsf1*fsf2)       #daughters
produced by males
  fsf<-(mfled*min(c(sum(density[1:3]),sum(density[4:6]))))*(msf1*msf2)    #sons produced by
females
  fsm<-(mfled*min(c(sum(density[1:3]),sum(density[4:6]))))*(msf1*msf2)  #sons produced by
males
```

```
 mat.mean<-matrix(c(0,0,fdf,0,0,fdm*mbp,
                fs11*fs12,0,0,0,0,0,
                0,fs21*fs22,fsa1*fsa2,0,0,0,
                0,0,fsf,0,0,fsm*mbp,
                0,0,0,ms11*ms12,0,0,
                0,0,0,0,ms21*ms22,msa1*msa2),
              byrow=T, nrow=6)
 density<-mat.mean%*%density
 N<-sum(density[1:6])
 r[i]<-log(N)
 density<-density/N}
lambdaS<-r[501]
lambdaS
exp(lambdaS) #population growth rate

#logit-transform mean values, and get standard deviation as 1/4th of the difference
#between the logit transformed confidence limits:
#-----------------------------------
MSfsa1<-c(log(0.979/(1-0.979)), ((log(0.991/(1-0.991)))-(log(0.955/(1-0.955))))/4)
MSfsa2<-c(log(0.962/(1-0.962)), ((log(0.979/(1-0.979)))-(log(0.930/(1-0.930))))/4)
MSfsf1<-c(log(0.671/(1-0.671)), ((log(0.822/(1-0.822)))-(log(0.521/(1-0.521))))/4)
MSfsf2<-c(log(0.602/(1-0.602)), ((log(0.790/(1-0.790)))-(log(0.414/(1-0.414))))/4)
MSfs11<-c(log(0.880/(1-0.880)), ((log(0.908/(1-0.908)))-(log(0.852/(1-0.852))))/4)
MSfs12<-c(log(0.868/(1-0.868)), ((log(0.928/(1-0.928)))-(log(0.807/(1-0.807))))/4)
MSfs21<-c(log(0.880/(1-0.880)), ((log(0.908/(1-0.908)))-(log(0.852/(1-0.852))))/4)
MSfs22<-c(log(0.868/(1-0.868)), ((log(0.928/(1-0.928)))-(log(0.807/(1-0.807))))/4)

MSmsa1<-c(log(0.979/(1-0.979)), ((log(0.991/(1-0.991)))-(log(0.955/(1-0.955))))/4)
MSmsa2<-c(log(0.962/(1-0.962)), ((log(0.979/(1-0.979)))-(log(0.930/(1-0.930))))/4)
MSmsf1<-c(log(0.671/(1-0.671)), ((log(0.822/(1-0.822)))-(log(0.521/(1-0.521))))/4)
MSmsf2<-c(log(0.602/(1-0.602)), ((log(0.790/(1-0.790)))-(log(0.414/(1-0.414))))/4)
MSms11<-c(log(0.880/(1-0.880)), ((log(0.908/(1-0.908)))-(log(0.852/(1-0.852))))/4)
MSms12<-c(log(0.868/(1-0.868)), ((log(0.928/(1-0.928)))-(log(0.807/(1-0.807))))/4)
MSms21<-c(log(0.880/(1-0.880)), ((log(0.908/(1-0.908)))-(log(0.852/(1-0.852))))/4)
MSms22<-c(log(0.868/(1-0.868)), ((log(0.928/(1-0.928)))-(log(0.807/(1-0.807))))/4)

MSffled<-c(log(0.340/(1-0.340)),((log(0.399/(1-0.399)))-(log(0.268/(1-0.268))))/4)
MSmfled<-c(log(0.120/(1-0.120)),((log(0.131/(1-0.131)))-(log(0.108/(1-0.108))))/4)
MSmbp<-c(log(0.793/(1-0.793)),  ((log(0.793/(1-0.793)))-(log(0.793/(1-0.793))))/4)

#sample survival rates from normal distribution, and back-transform to ordinary scale
#'repeats' is the number of samples drawn

repeats<-10000

logitfsa1<-rnorm(repeats,MSfsa1[1],MSfsa1[2])
fsa1<-exp(logitfsa1)/(1+exp(logitfsa1))
logitfsa2<-rnorm(repeats,MSfsa2[1],MSfsa2[2])
fsa2<-exp(logitfsa2)/(1+exp(logitfsa2))
```

```
logitfsf1<-rnorm(repeats,MSfsf1[1],MSfsf1[2])
fsf1<-exp(logitfsf1)/(1+exp(logitfsf1))
logitfsf2<-rnorm(repeats,MSfsf2[1],MSfsf2[2])
fsf2<-exp(logitfsf2)/(1+exp(logitfsf2))
logitfs11<-rnorm(repeats,MSfs11 [1],MSfs11[2])
fs11<-exp(logitfs11)/(1+exp(logitfs11))
logitfs12<-rnorm(repeats,MSfs12[1],MSfs12[2])
fs12<-exp(logitfs12)/(1+exp(logitfs12))
logitfs21<-rnorm(repeats,MSfs21[1],MSfs21[2])
fs21<-exp(logitfs21)/(1+exp(logitfs21))
logitfs22<-rnorm(repeats,MSfs22[1],MSfs22[2])
fs22<-exp(logitfs22)/(1+exp(logitfs22))
logitmsa1<-rnorm(repeats,MSmsa1[1],MSmsa1[2])
msa1<-exp(logitmsa1)/(1+exp(logitmsa1))
logitmsa2<-rnorm(repeats,MSmsa2[1],MSmsa2[2])
msa2<-exp(logitmsa2)/(1+exp(logitmsa2))
logitmsf1<-rnorm(repeats,MSmsf1[1],MSmsf1[2])
msf1<-exp(logitmsf1)/(1+exp(logitmsf1))
logitmsf2<-rnorm(repeats,MSmsf2[1],MSmsf2[2])
msf2<-exp(logitmsf2)/(1+exp(logitmsf2))
logitms11<-rnorm(repeats,MSms11 [1],MSms11[2])
ms11<-exp(logitms11)/(1+exp(logitms11))
logitms12<-rnorm(repeats,MSms12[1],MSms12[2])
ms12<-exp(logitms12)/(1+exp(logitms12))
logitms21<-rnorm(repeats,MSms21[1],MSms21[2])
ms21<-exp(logitms21)/(1+exp(logitms21))
logitms22<-rnorm(repeats,MSms22[1],MSms22[2])
ms22<-exp(logitms22)/(1+exp(logitms22))
logitffled<-rnorm(repeats,MSffled[1],MSffled[2])
ffled<-exp(logitffled)/(1+exp(logitffled))
logitmfled<-rnorm(repeats,MSmfled[1],MSmfled[2])
mfled<-exp(logitmfled)/(1+exp(logitmfled))
logitmbp<-rnorm(repeats,MSmbp[1],MSmbp[2])
mbp<-exp(logitmbp)/(1+exp(logitmbp))

lambda.r <- rep(NA, repeats)
fdf<-rep(NA, repeats)
fdm<-rep(NA, repeats)
fsf<-rep(NA, repeats)
fsm<-rep(NA, repeats)

for(j in 1:repeats) {
 # simulation to estimate population growth rate
 ts.length<-502  #set desired length of time series
 r<-rep(NA,ts.length-1)
 density<-rep(1/6,6)   #adds starting values for population vector
 N<-sum(density)

 for (i in 1:(ts.length-1)) {
```

```
   fdf[j]<-(ffled[j]*min(c(sum(density[1:3]),sum(density[4:6])))*(fsf1[j]*fsf2[j])
   fdm[j]<-(ffled[j]*min(c(sum(density[1:3]),sum(density[4:6])))*(fsf1[j]*fsf2[j])
   fsf[j]<-(mfled[j]*min(c(sum(density[1:3]),sum(density[4:6])))*(msf1[j]*msf2[j])
   fsm[j]<-(mfled[j]*min(c(sum(density[1:3]),sum(density[4:6])))*(msf1[j]*msf2[j])

   mat.r <-matrix(c(0,0,fdf[j],0,0,fdm[j]*mbp[j],
                fs11[j]*fs12[j],0,0,0,0,0,
                0,fs21[j]*fs22[j],fsa1[j]*fsa2[j],0,0,0,
                0,0,fsf[j],0,0,fsm[j]*mbp[j],
                0,0,0,ms11[j]*ms12[j],0,0,
                0,0,0,0,ms21[j]*ms22[j],msa1[j]*msa2[j]),
              byrow=T, nrow=6)
   density<-mat.r%*%density
   N<-sum(density[1:6])
   r[i]<-log(N)
   density<-density/N}
  lambda.r[j]<-r[501]
}

hist(lambda.r-lambdaS)
exp(lambda.r)
tran.r<-exp(lambda.r)
tran.rs<-sort(tran.r, decreasing = FALSE)
lcl <- tran.rs[c(250)]
ucl <- tran.rs[c(9750)]
lcl #lower confidence limits
ucl #upper confidence limits
```

Appendix E: Sheathbill population projections (Chapter 3)

Appendix E1: Baseline model

Year 1 begins on the 4th run of the matrix
#Starting values of scenarios differ so that the number of adults are equal at year 1

```
#-------------------------------------------------------------------------------------------
#Base model parameters
#-------------------------------------------------------------------------------------------
Kk <- 200 # carrying capacity in king penguin colonies
Kr <- 1000 # carrying capacity in rh penguin colonies
Tm <- 303 # length of time series
psi.kr <- 0
psi.rk <- 0
mmove.kr <- rep(NA,Tm-1) #male movement
fmove.kr <- rep(NA,Tm-1) #female movement

#RH Sheathbill Females
#-----------------------------------------------------------------------
rhfsa1 <-  0.981 # breeding adult survival season 1
rhfsa2 <-  0.962  # breeding adult survival season 2
rhfsf1 <-  0.636 # fledgling survival season 1
rhfsf2 <-  0.558   # fledgling survival season 2
rhfs11 <-  0.874   # one-year olds survival season 1
rhfs12 <-  0.853 # one-year olds survival season 2
rhfs21 <-  0.874  # two-year olds survival season 1
rhfs22 <-  0.853  # two-year olds survival season 2
rhfn0<-c(88,88,1645)

#RH Sheathbill Males
#-----------------------------------------------------------------------
rhmsa1 <-  0.981 # breeding adult survival season 1
rhmsa2 <-  0.962  # breeding adult survival season 2
rhmsf1 <-  0.636 # fledgling survival season 1
rhmsf2  <-  0.558   # fledgling survival season 2
rhms11  <-  0.874   # one-year olds survival season 1
rhms12 <-  0.853 # one-year olds survival season 2
rhms21 <-  0.874  # two-year olds survival season 1
rhms22 <-  0.853  # two-year olds survival season 2
rhmn0<-c(22,22,1478)

#RH Sheathbill reproduction
#-------------------------------------------------------------

rhffled <- 0.34   # number of females produced by each sex
rhmfled <- 0.11   # number of males produced by each sex
rhnf<-seq(1,3)
rhnm<-seq(1,3)
```

```
rhfdf<-(rhffled*(sum(rhnm)/(sum(rhnf)+sum(rhnm))))*(rhfsf1*rhfsf2) #daughters produced
by females
rhfdm<-(rhffled*(sum(rhnf)/(sum(rhnf)+sum(rhnm))))*(rhfsf1*rhfsf2) #daughters produced
by males
rhfsf<-(rhmfled*(sum(rhnm)/(sum(rhnf)+sum(rhnm))))*(rhmsf1*rhmsf2) #sons produced by
females
rhfsm<-(rhmfled*(sum(rhnf)/(sum(rhnf)+sum(rhnm))))*(rhmsf1*rhmsf2) #sons produced by
males

#KP Sheathbill Females
#------------------------------------------------------------------------
kpfsa1 <-  0.979 # breeding adult survival season 1
kpfsa2 <-  0.959  # breeding adult survival season 2
kpfsf1 <-  0.838 # fledgling survival season 1
kpfsf2  <-  0.811   # fledgling survival season 2
kpfs11  <-  0.935   # one-year olds survival season 1
kpfs12 <-  0.912 # one-year olds survival season 2
kpfs21 <-  0.935  # two-year olds survival season 1
kpfs22 <-  0.912  # two-year olds survival season 2
kpfn0<-c(16,16,200)

#KP Sheathbill Males
#------------------------------------------------------------------------
kpmsa1 <-  0.979 # breeding adult survival season 1
kpmsa2 <-  0.959  # breeding adult survival season 2
kpmsf1 <-  0.838 # fledgling survival season 1
kpmsf2 <-  0.811   # fledgling survival season 2
kpms11 <-  0.935   # one-year olds survival season 1
kpms12 <-  0.912 # one-year olds survival season 2
kpms21 <-  0.935  # two-year olds survival season 1
kpms22 <-  0.912  # two-year olds survival season 2
kpmn0<-c(16,16,200)

#KP Sheathbill reproduction
#------------------------------------------------------------------------
kpffled <- 0.37   # number of females by each sex
kpmfled <- 0.155  # number of males be each sex
kpnf<-seq(1,3)
kpnm<-seq(1,3)
kpfdf<-(kpffled*(sum(kpnm)/(sum(kpnf)+sum(kpnm))))*(kpfsf1*kpfsf2) #daughters
produced by females
kpfdm<-(kpffled*(sum(kpnf)/(sum(kpnf)+sum(kpnm))))*(kpfsf1*kpfsf2) #daughters
produced by males
kpfsf<-(kpmfled*(sum(kpnm)/(sum(kpnf)+sum(kpnm))))*(kpmsf1*kpmsf2) #sons produced
by females
kpfsm<-(kpmfled*(sum(kpnf)/(sum(kpnf)+sum(kpnm))))*(kpmsf1*kpmsf2) #sons produced
by males

#for counting fledgers
```

```
#-------------------------------------------------------------------------------------
rhfdfc<-(rhffled*(sum(rhnm)/(sum(rhnf)+sum(rhnm))))*(rhfsf1*rhfsf2)
rhfdmc<-(rhffled*(sum(rhnf)/(sum(rhnf)+sum(rhnm))))*(rhfsf1*rhfsf2)
rhfsfc<-(rhmfled*(sum(rhnm)/(sum(rhnf)+sum(rhnm))))*(rhmsf1*rhmsf2)
rhfsmc<-(rhmfled*(sum(rhnm)/(sum(rhnf)+sum(rhnm))))*(rhmsf1*rhmsf2)
kpfdfc<-(kpffled*(sum(kpnm)/(sum(kpnf)+sum(kpnm))))*(kpfsf1*kpfsf2)
kpfdmc<-(kpffled*(sum(kpnm)/(sum(kpnf)+sum(kpnm))))*(kpfsf1*kpfsf2)
kpfsfc<-(kpmfled*(sum(kpnf)/(sum(kpnf)+sum(kpnm))))*(kpmsf1*kpmsf2)
kpfsmc<-(kpmfled*(sum(kpnf)/(sum(kpnf)+sum(kpnm))))*(kpmsf1*kpmsf2)

A <-  matrix(c(0,0,rhfdf,0,0,rhfdm,0,0,0,0,0,0,
          rhfs11*rhfs12,0,0,0,0,0,0,0,0,0,0,0,
          0,(1-psi.rk)*rhfs21*rhfs22,rhfsa1*rhfsa2,0,0,0,0,psi.kr*kpfs21*kpfs22,0,0,0,0,
          0,0,rhfsf,0,0,rhfsm,0,0,0,0,0,0,
          0,0,0,rhms11*rhms12,0,0,0,0,0,0,0,0,
          0,0,0,0,(1-
psi.rk)*rhms21*rhms22,rhmsa1*rhmsa2,0,0,0,0,psi.kr*kpms21*kpms22,0,
          0,0,0,0,0,0,0,0,kpfdf,0,0,kpfdm,
          0,0,0,0,0,0,kpfs11*kpfs12,0,0,0,0,0,
          0,psi.rk*rhfs21*rhfs22,0,0,0,0,0,(1-psi.kr)*kpfs21*kpfs22,kpfsa1*kpfsa2,0,0,0,
          0,0,0,0,0,0,0,0,kpfsf,0,0,kpfsm,
          0,0,0,0,0,0,0,0,0,kpms11*kpms12,0,0,
          0,0,0,0,psi.rk*rhms21*rhms22,0,0,0,0,0,(1-
psi.kr)*kpms21*kpms22,kpmsa1*kpmsa2),
         byrow=T, nrow=12)

#simulation to estimate population growth rate when sex ratio not fixed: limited by rarer sex
#-------------------------------------------------------------------------------------
Kk <- 200 # carrying capacity in king penguin colonies
Kr <- 1000 # carrying capacity in rh penguin colonies
Tm <- 303 # length of time series
psi.kr <- 0
psi.rk <- 0
n0 <- c(rhfn0, rhmn0, kpfn0, kpmn0) # starting population values

n <- matrix(NA, nrow = length(n0),ncol=Tm)
n[,1] <- n0
rhmbp <-Kr/n[6]#breeding probability of rockhopper males

A <-  matrix(c(0,0,rhfdf,0,0,rhfdm*rhmbp,0,0,0,0,0,0,
          rhfs11*rhfs12,0,0,0,0,0,0,0,0,0,0,0,
          0,(1-psi.rk)*rhfs21*rhfs22,rhfsa1*rhfsa2,0,0,0,0,psi.kr*kpfs21*kpfs22,0,0,0,0,
          0,0,rhfsf,0,0,rhfsm*rhmbp,0,0,0,0,0,0,
          0,0,0,rhms11*rhms12,0,0,0,0,0,0,0,0,
          0,0,0,0,(1-
psi.rk)*rhms21*rhms22,rhmsa1*rhmsa2,0,0,0,0,psi.kr*kpms21*kpms22,0,
          0,0,0,0,0,0,0,0,kpfdf,0,0,kpfdm,
          0,0,0,0,0,0,kpfs11*kpfs12,0,0,0,0,0,
          0,psi.rk*rhfs21*rhfs22,0,0,0,0,0,(1-psi.kr)*kpfs21*kpfs22,kpfsa1*kpfsa2,0,0,0,
```

```
            0,0,0,0,0,0,0,0,kpfsf,0,0,kpfsm,
            0,0,0,0,0,0,0,0,0,kpms11*kpms12,0,0,
            0,0,0,0,psi.rk*rhms21*rhms22,0,0,0,0,0,(1-
psi.kr)*kpms21*kpms22,kpmsa1*kpmsa2),
          byrow=T, nrow=12)

for (i in 2:Tm) {
  n[,i] = A %*% n[,i-1]
  mmove.kr[i] <- ifelse(n[12,i-1]<Kk, 0, (n[12,i] - Kk))
  fmove.kr[i] <- ifelse(n[9,i-1]<Kk, 0, (n[9,i] - Kk))
  n[3,i] <- n[3,i] + fmove.kr[i]
  n[6,i] <- n[6,i] + mmove.kr[i]
  n[9,i] <- n[9,i] - fmove.kr[i]
  n[12,i] <- n[12,i] - mmove.kr[i]
  rhmbp[i] <- ifelse((Kr/n[6,i])>1, 1,(Kr/n[6,i]))
  rhfdf[i]<-(rhffled*min(c((n[3,i])/(n[3,i]+n[6,i])),((n[6,i])/(n[3,i]+n[6,i])))*(rhfsf1*rhfsf2) #rh
daughters by females
  rhfdm[i]<-(rhffled*min(c((n[3,i])/(n[3,i]+n[6,i])),((n[6,i])/(n[3,i]+n[6,i])))*(rhfsf1*rhfsf2) #rh
daughters by males
  rhfsf[i]<-(rhmfled*min(c((n[3,i])/(n[3,i]+n[6,i])),((n[6,i])/(n[3,i]+n[6,i])))*(rhmsf1*rhmsf2)
#rh sons by females
  rhfsm[i]<-(rhmfled*min(c((n[3,i])/(n[3,i]+n[6,i])),((n[6,i])/(n[3,i]+n[6,i])))*(rhmsf1*rhmsf2)
#rh sons by males
  kpfdf[i]<-(kpffled*min(c((n[9,i])/(n[9,i]+n[12,i])),((n[12,i])/(n[9,i]+n[12,i])))*(kpfsf1*kpfsf2)
#kp daughters by females
  kpfdm[i]<-(kpffled*min(c((n[9,i])/(n[9,i]+n[12,i])),((n[12,i])/(n[9,i]+n[12,i])))*(kpfsf1*kpfsf2)
#kp daughters by males
  kpfsf[i]<-
(kpmfled*min(c((n[9,i])/(n[9,i]+n[12,i])),((n[12,i])/(n[9,i]+n[12,i])))*(kpmsf1*kpmsf2) #kp
sons by females
  kpfsm[i]<-
(kpmfled*min(c((n[9,i])/(n[9,i]+n[12,i])),((n[12,i])/(n[9,i]+n[12,i])))*(kpmsf1*kpmsf2) #kp
sons by males
  rhfdfc[i]<-(rhffled*min(c((n[3,i])/(n[3,i]+n[6,i])),((n[6,i])/(n[3,i]+n[6,i])))*(n[3,i]) #for count
  rhfdmc[i]<-(rhffled*min(c((n[3,i])/(n[3,i]+n[6,i])),((n[6,i])/(n[3,i]+n[6,i])))*(n[3,i]) #for count
  rhfsfc[i]<-(rhmfled*min(c((n[3,i])/(n[3,i]+n[6,i])),((n[6,i])/(n[3,i]+n[6,i])))*(n[6,i]) #for count
  rhfsmc[i]<-(rhmfled*min(c((n[3,i])/(n[3,i]+n[6,i])),((n[6,i])/(n[3,i]+n[6,i])))*(n[6,i]) #for
count
  kpfdfc[i]<-(kpffled*min(c((n[9,i])/(n[9,i]+n[12,i])),((n[12,i])/(n[9,i]+n[12,i])))*(n[9,i]) #for
count
  kpfdmc[i]<-(kpffled*min(c((n[9,i])/(n[9,i]+n[12,i])),((n[12,i])/(n[9,i]+n[12,i])))*(n[9,i]) #for
count
  kpfsfc[i]<-(kpmfled*min(c((n[9,i])/(n[9,i]+n[12,i])),((n[12,i])/(n[9,i]+n[12,i])))*(n[12,i]) #for
count
  kpfsmc[i]<-(kpmfled*min(c((n[9,i])/(n[9,i]+n[12,i])),((n[12,i])/(n[9,i]+n[12,i])))*(n[12,i]) #for
count
}

#sum columns and plot
```

```
total1<- colSums(n)   #all subadults and adults
total2<-rhfdfc+rhfdmc+rhfsfc+rhfsmc+kpfdfc+kpfdmc+kpfsfc+kpfsmc   #all juveniles
total3<-total1+total2   #all birds
plot(total3, type='l',ylim=c(0,max(total3)), col='black')
lines(n[3,], col='red',lines(n[6,],col='blue',lines(n[9,], col='purple',lines(n[12,],
col='green',lines(total3)))))
```

```
 (n[c(1,2,3,4,5,6,7,8,9,10,11,12),])  # number of subadult RH females (1,2), adult RH females
(3), subadult RH males (4,5), adult RH males (6), subadult KP females (7,8), adult KP females
(9), subadult KP males (10,11), and adult KP males (12)

total3 #absolute number of sheathbills
```

Appendix E2: Sheathbill population projection, 500 RH nesting sites model parameters

```
#-------------------------------------------------------------------------------------------
Kk <- 200 # carrying capacity in king penguin colonies
Kr <- 500 # carrying capacity in rh penguin colonies
Tm <- 303 # length of time series
psi.kr <- 0
psi.rk <- 0
mmove.kr <- rep(NA,Tm-1) #male movement
fmove.kr <- rep(NA,Tm-1) #female movement

#RH Sheathbill Females
#-----------------------------------------------------------------------
rhfsa1 <-  0.981 # breeding adult survival season 1
rhfsa2 <-  0.962  # breeding adult survival season 2
rhfsf1 <-  0.636 # fledgling survival season 1
rhfsf2 <-  0.558   # fledgling survival season 2
rhfs11 <-  0.874   # one-year olds survival season 1
rhfs12 <-  0.853 # one-year olds survival season 2
rhfs21 <-  0.874  # two-year olds survival season 1
rhfs22 <-  0.853  # two-year olds survival season 2

rhfn0<-c(88,88,1665)

#RH Sheathbill Males
#-----------------------------------------------------------------------
rhmsa1 <-  0.981 # breeding adult survival season 1
rhmsa2 <-  0.962  # breeding adult survival season 2
rhmsf1 <-  0.636 # fledgling survival season 1
rhmsf2  <-  0.558   # fledgling survival season 2
rhms11  <-  0.874   # one-year olds survival season 1
rhms12 <-  0.853 # one-year olds survival season 2
rhms21 <-  0.874  # two-year olds survival season 1
rhms22 <-  0.853  # two-year olds survival season 2
rhmn0<-c(22,22,1483)

#RH Sheathbill reproduction
#-------------------------------------------------------------

rhffled <- 0.34   # number of females produced by each sex
rhmfled <- 0.11   # number of males produced by each sex
rhnf<-seq(1,3)
rhnm<-seq(1,3)
rhfdf<-(rhffled*(sum(rhnm)/(sum(rhnf)+sum(rhnm))))*(rhfsf1*rhfsf2) #daughters produced
by females
rhfdm<-(rhffled*(sum(rhnf)/(sum(rhnf)+sum(rhnm))))*(rhfsf1*rhfsf2) #daughters produced
by males
rhfsf<-(rhmfled*(sum(rhnm)/(sum(rhnf)+sum(rhnm))))*(rhmsf1*rhmsf2) #sons produced by
females
```

```
rhfsm<-(rhmfled*(sum(rhnf)/(sum(rhnf)+sum(rhnm))))*(rhmsf1*rhmsf2) #sons produced by
males

#KP Sheathbill Females
#------------------------------------------------------------------------
kpfsa1 <-  0.979 # breeding adult survival season 1
kpfsa2 <-  0.959  # breeding adult survival season 2
kpfsf1 <-  0.838 # fledgling survival season 1
kpfsf2  <-  0.811   # fledgling survival season 2
kpfs11  <-  0.935   # one-year olds survival season 1
kpfs12 <-  0.912 # one-year olds survival season 2
kpfs21 <-  0.935  # two-year olds survival season 1
kpfs22 <-  0.912  # two-year olds survival season 2
kpfn0<-c(16,16,200)

#KP Sheathbill Males
#-------------------------------------------------------------------------
kpmsa1 <-  0.979 # breeding adult survival season 1
kpmsa2 <-  0.959  # breeding adult survival season 2
kpmsf1 <-  0.838 # fledgling survival season 1
kpmsf2 <-  0.811   # fledgling survival season 2
kpms11 <-  0.935   # one-year olds survival season 1
kpms12 <-  0.912 # one-year olds survival season 2
kpms21 <-  0.935  # two-year olds survival season 1
kpms22 <-  0.912  # two-year olds survival season 2
kpmn0<-c(16,16,200)

#KP Sheathbill reproduction
#------------------------------------------------------------------------
kpffled <- 0.37   # number of females by each sex
kpmfled <- 0.155  # number of males be each sex
kpnf<-seq(1,3)
kpnm<-seq(1,3)
kpfdf<-(kpffled*(sum(kpnm)/(sum(kpnf)+sum(kpnm))))*(kpfsf1*kpfsf2) #daughters
produced by females
kpfdm<-(kpffled*(sum(kpnf)/(sum(kpnf)+sum(kpnm))))*(kpfsf1*kpfsf2) #daughters
produced by males
kpfsf<-(kpmfled*(sum(kpnm)/(sum(kpnf)+sum(kpnm))))*(kpmsf1*kpmsf2) #sons produced
by females
kpfsm<-(kpmfled*(sum(kpnf)/(sum(kpnf)+sum(kpnm))))*(kpmsf1*kpmsf2) #sons produced
by males

#for counting fledgers
#---------------------------------------------------------------------------------
rhfdfc<-(rhffled*(sum(rhnm)/(sum(rhnf)+sum(rhnm))))*(rhfsf1*rhfsf2)
rhfdmc<-(rhffled*(sum(rhnf)/(sum(rhnf)+sum(rhnm))))*(rhfsf1*rhfsf2)
rhfsfc<-(rhmfled*(sum(rhnm)/(sum(rhnf)+sum(rhnm))))*(rhmsf1*rhmsf2)
rhfsmc<-(rhmfled*(sum(rhnm)/(sum(rhnf)+sum(rhnm))))*(rhmsf1*rhmsf2)
kpfdfc<-(kpffled*(sum(kpnm)/(sum(kpnf)+sum(kpnm))))*(kpfsf1*kpfsf2)
```

```
kpfdmc<-(kpffled*(sum(kpnm)/(sum(kpnf)+sum(kpnm))))*(kpfsf1*kpfsf2)
kpfsfc<-(kpmfled*(sum(kpnf)/(sum(kpnf)+sum(kpnm))))*(kpmsf1*kpmsf2)
kpfsmc<-(kpmfled*(sum(kpnf)/(sum(kpnf)+sum(kpnm))))*(kpmsf1*kpmsf2)

A <-  matrix(c(0,0,rhfdf,0,0,rhfdm,0,0,0,0,0,0,
          rhfs11*rhfs12,0,0,0,0,0,0,0,0,0,0,0,
          0,(1-psi.rk)*rhfs21*rhfs22,rhfsa1*rhfsa2,0,0,0,0,psi.kr*kpfs21*kpfs22,0,0,0,0,
          0,0,rhfsf,0,0,rhfsm,0,0,0,0,0,0,
          0,0,0,rhms11*rhms12,0,0,0,0,0,0,0,0,
          0,0,0,0,(1-
psi.rk)*rhms21*rhms22,rhmsa1*rhmsa2,0,0,0,0,psi.kr*kpms21*kpms22,0,
          0,0,0,0,0,0,0,0,kpfdf,0,0,kpfdm,
          0,0,0,0,0,0,0,kpfs11*kpfs12,0,0,0,0,0,0,
          0,psi.rk*rhfs21*rhfs22,0,0,0,0,0,(1-psi.kr)*kpfs21*kpfs22,kpfsa1*kpfsa2,0,0,0,
          0,0,0,0,0,0,0,0,0,kpfsf,0,0,kpfsm,
          0,0,0,0,0,0,0,0,0,0,kpms11*kpms12,0,0,
          0,0,0,0,psi.rk*rhms21*rhms22,0,0,0,0,0,(1-
psi.kr)*kpms21*kpms22,kpmsa1*kpmsa2),
         byrow=T, nrow=12)

#simulation to estimate population growth rate when sex ratio not fixed: limited by rarer sex
#-----------------------------------------------------------------------------------------
Kk <- 200 # carrying capacity in king penguin colonies
Kr <- 500 # carrying capacity in rh penguin colonies
Tm <- 303 # length of time series
psi.kr <- 0
psi.rk <- 0
n0 <- c(rhfn0, rhmn0, kpfn0, kpmn0) # starting population values

n <- matrix(NA, nrow = length(n0),ncol=Tm)
n[,1] <- n0
rhmbp <-Kr/n[6]#breeding probability of rockhopper males

A <-  matrix(c(0,0,rhfdf,0,0,rhfdm*rhmbp,0,0,0,0,0,0,
          rhfs11*rhfs12,0,0,0,0,0,0,0,0,0,0,0,
          0,(1-psi.rk)*rhfs21*rhfs22,rhfsa1*rhfsa2,0,0,0,0,psi.kr*kpfs21*kpfs22,0,0,0,0,
          0,0,rhfsf,0,0,rhfsm*rhmbp,0,0,0,0,0,0,
          0,0,0,rhms11*rhms12,0,0,0,0,0,0,0,0,
          0,0,0,0,(1-
psi.rk)*rhms21*rhms22,rhmsa1*rhmsa2,0,0,0,0,psi.kr*kpms21*kpms22,0,
          0,0,0,0,0,0,0,0,kpfdf,0,0,kpfdm,
          0,0,0,0,0,0,0,kpfs11*kpfs12,0,0,0,0,0,0,
          0,psi.rk*rhfs21*rhfs22,0,0,0,0,0,(1-psi.kr)*kpfs21*kpfs22,kpfsa1*kpfsa2,0,0,0,
          0,0,0,0,0,0,0,0,0,kpfsf,0,0,kpfsm,
          0,0,0,0,0,0,0,0,0,0,kpms11*kpms12,0,0,
          0,0,0,0,psi.rk*rhms21*rhms22,0,0,0,0,0,(1-
psi.kr)*kpms21*kpms22,kpmsa1*kpmsa2),
         byrow=T, nrow=12)
```

```
for (i in 2:Tm) {
  n[,i] = A %*% n[,i-1]
  mmove.kr[i] <- ifelse(n[12,i-1]<Kk, 0, (n[12,i] - Kk))
  fmove.kr[i] <- ifelse(n[9,i-1]<Kk, 0, (n[9,i] - Kk))
  n[3,i] <- n[3,i] + fmove.kr[i]
  n[6,i] <- n[6,i] + mmove.kr[i]
  n[9,i] <- n[9,i] - fmove.kr[i]
  n[12,i] <- n[12,i] - mmove.kr[i]
  rhmbp[i] <- ifelse((Kr/n[6,i])>1, 1,(Kr/n[6,i]))
  rhfdf[i]<-(rhffled*min(c((n[3,i])/(n[3,i]+n[6,i])),((n[6,i])/(n[3,i]+n[6,i])))*(rhfsf1*rhfsf2) #rh
daughters by females
  rhfdm[i]<-(rhffled*min(c((n[3,i])/(n[3,i]+n[6,i])),((n[6,i])/(n[3,i]+n[6,i])))*(rhfsf1*rhfsf2) #rh
daughters by males
  rhfsf[i]<-(rhmfled*min(c((n[3,i])/(n[3,i]+n[6,i])),((n[6,i])/(n[3,i]+n[6,i])))*(rhmsf1*rhmsf2)
#rh sons by females
  rhfsm[i]<-(rhmfled*min(c((n[3,i])/(n[3,i]+n[6,i])),((n[6,i])/(n[3,i]+n[6,i])))*(rhmsf1*rhmsf2)
#rh sons by males
  kpfdf[i]<-(kpffled*min(c((n[9,i])/(n[9,i]+n[12,i])),((n[12,i])/(n[9,i]+n[12,i])))*(kpfsf1*kpfsf2)
#kp daughters by females
  kpfdm[i]<-(kpffled*min(c((n[9,i])/(n[9,i]+n[12,i])),((n[12,i])/(n[9,i]+n[12,i])))*(kpfsf1*kpfsf2)
#kp daughters by males
  kpfsf[i]<-
(kpmfled*min(c((n[9,i])/(n[9,i]+n[12,i])),((n[12,i])/(n[9,i]+n[12,i])))*(kpmsf1*kpmsf2) #kp
sons by females
  kpfsm[i]<-
(kpmfled*min(c((n[9,i])/(n[9,i]+n[12,i])),((n[12,i])/(n[9,i]+n[12,i])))*(kpmsf1*kpmsf2) #kp
sons by males
  rhfdfc[i]<-(rhffled*min(c((n[3,i])/(n[3,i]+n[6,i])),((n[6,i])/(n[3,i]+n[6,i])))*(n[3,i]) #for count
  rhfdmc[i]<-(rhffled*min(c((n[3,i])/(n[3,i]+n[6,i])),((n[6,i])/(n[3,i]+n[6,i])))*(n[3,i]) #for count
  rhfsfc[i]<-(rhmfled*min(c((n[3,i])/(n[3,i]+n[6,i])),((n[6,i])/(n[3,i]+n[6,i])))*(n[6,i]) #for count
  rhfsmc[i]<-(rhmfled*min(c((n[3,i])/(n[3,i]+n[6,i])),((n[6,i])/(n[3,i]+n[6,i])))*(n[6,i]) #for
count
  kpfdfc[i]<-(kpffled*min(c((n[9,i])/(n[9,i]+n[12,i])),((n[12,i])/(n[9,i]+n[12,i])))*(n[9,i]) #for
count
  kpfdmc[i]<-(kpffled*min(c((n[9,i])/(n[9,i]+n[12,i])),((n[12,i])/(n[9,i]+n[12,i])))*(n[9,i]) #for
count
  kpfsfc[i]<-(kpmfled*min(c((n[9,i])/(n[9,i]+n[12,i])),((n[12,i])/(n[9,i]+n[12,i])))*(n[12,i]) #for
count
  kpfsmc[i]<-(kpmfled*min(c((n[9,i])/(n[9,i]+n[12,i])),((n[12,i])/(n[9,i]+n[12,i])))*(n[12,i]) #for
count
}

#sum columns and plot
total1<- colSums(n)   #all subadults and adults
total2<-rhfdfc+rhfdmc+rhfsfc+rhfsmc+kpfdfc+kpfdmc+kpfsfc+kpfsmc   #all fledgers
total3<-total1+total2   #all birds

plot(total3, type='l',ylim=c(0,max(total3)), col='black')
```

```
lines(n[3,], col='red',lines(n[6,],col='blue',lines(n[9,], col='purple',lines(n[12,],
col='green',lines(total3)))))

(n[c(1,2,3,4,5,6,7,8,9,10,11,12),]) # number of subadult RH females (1,2), adult RH females
(3), subadult RH males (4,5), adult RH males (6), subadult KP females (7,8), adult KP females
(9), subadult KP males (10,11), and adult KP males (12)

total3 #absolute population size
```

Appendix E3: Sheathbill population projection, 250 RH nesting sites model parameters

```
#-------------------------------------------------------------------------------------------
Kk <- 200 # carrying capacity in king penguin colonies
Kr <- 250 # carrying capacity in rh penguin colonies
Tm <- 303 # length of time series
psi.kr <- 0
psi.rk <- 0
mmove.kr <- rep(NA,Tm-1) #male movement
fmove.kr <- rep(NA,Tm-1) #female movement

#RH Sheathbill Females
#-----------------------------------------------------------------------
rhfsa1 <-  0.981 # breeding adult survival season 1
rhfsa2 <-  0.962  # breeding adult survival season 2
rhfsf1 <-  0.636 # fledgling survival season 1
rhfsf2 <-  0.558   # fledgling survival season 2
rhfs11 <-  0.874   # one-year olds survival season 1
rhfs12 <-  0.853 # one-year olds survival season 2
rhfs21 <-  0.874  # two-year olds survival season 1
rhfs22 <-  0.853  # two-year olds survival season 2
rhfn0<-c(88,88,1673)

#RH Sheathbill Males
#-----------------------------------------------------------------------
rhmsa1 <-  0.981 # breeding adult survival season 1
rhmsa2 <-  0.962  # breeding adult survival season 2
rhmsf1 <-  0.636 # fledgling survival season 1
rhmsf2  <-  0.558   # fledgling survival season 2
rhms11  <-  0.874   # one-year olds survival season 1
rhms12 <-  0.853 # one-year olds survival season 2
rhms21 <-  0.874  # two-year olds survival season 1
rhms22 <-  0.853  # two-year olds survival season 2
rhmn0<-c(22,22,1486)

#RH Sheathbill reproduction
#-------------------------------------------------------------
rhffled <- 0.34   # number of females produced by each sex
rhmfled <- 0.11   # number of males produced by each sex
rhnf<-seq(1,3)
rhnm<-seq(1,3)
rhfdf<-(rhffled*(sum(rhnm)/(sum(rhnf)+sum(rhnm))))*(rhfsf1*rhfsf2) #daughters produced
by females
rhfdm<-(rhffled*(sum(rhnf)/(sum(rhnf)+sum(rhnm))))*(rhfsf1*rhfsf2) #daughters produced
by males
rhfsf<-(rhmfled*(sum(rhnm)/(sum(rhnf)+sum(rhnm))))*(rhmsf1*rhmsf2) #sons produced by
females
rhfsm<-(rhmfled*(sum(rhnf)/(sum(rhnf)+sum(rhnm))))*(rhmsf1*rhmsf2) #sons produced by
males
```

```
#KP Sheathbill Females
#------------------------------------------------------------------------
kpfsa1 <-  0.979 # breeding adult survival season 1
kpfsa2 <-  0.959  # breeding adult survival season 2
kpfsf1 <-  0.838 # fledgling survival season 1
kpfsf2  <-  0.811   # fledgling survival season 2
kpfs11  <-  0.935   # one-year olds survival season 1
kpfs12 <-  0.912 # one-year olds survival season 2
kpfs21 <-  0.935  # two-year olds survival season 1
kpfs22 <-  0.912  # two-year olds survival season 2
kpfn0<-c(16,16,200)

#KP Sheathbill Males
#------------------------------------------------------------------------
kpmsa1 <-  0.979 # breeding adult survival season 1
kpmsa2 <-  0.959  # breeding adult survival season 2
kpmsf1 <-  0.838 # fledgling survival season 1
kpmsf2 <-  0.811   # fledgling survival season 2
kpms11 <-  0.935   # one-year olds survival season 1
kpms12 <-  0.912 # one-year olds survival season 2
kpms21 <-  0.935  # two-year olds survival season 1
kpms22 <-  0.912  # two-year olds survival season 2
kpmn0<-c(16,16,200)

#KP Sheathbill reproduction
#------------------------------------------------------------------------
kpffled <- 0.37   # number of females by each sex
kpmfled <- 0.155  # number of males be each sex
kpnf<-seq(1,3)
kpnm<-seq(1,3)
kpfdf<-(kpffled*(sum(kpnm)/(sum(kpnf)+sum(kpnm))))*(kpfsf1*kpfsf2) #daughters
produced by females
kpfdm<-(kpffled*(sum(kpnf)/(sum(kpnf)+sum(kpnm))))*(kpfsf1*kpfsf2) #daughters
produced by males
kpfsf<-(kpmfled*(sum(kpnm)/(sum(kpnf)+sum(kpnm))))*(kpmsf1*kpmsf2) #sons produced
by females
kpfsm<-(kpmfled*(sum(kpnf)/(sum(kpnf)+sum(kpnm))))*(kpmsf1*kpmsf2) #sons produced
by males

#for counting fledgers
#------------------------------------------------------------------------------------
rhfdfc<-(rhffled*(sum(rhnm)/(sum(rhnf)+sum(rhnm))))*(rhfsf1*rhfsf2)
rhfdmc<-(rhffled*(sum(rhnf)/(sum(rhnf)+sum(rhnm))))*(rhfsf1*rhfsf2)
rhfsfc<-(rhmfled*(sum(rhnm)/(sum(rhnf)+sum(rhnm))))*(rhmsf1*rhmsf2)
rhfsmc<-(rhmfled*(sum(rhnm)/(sum(rhnf)+sum(rhnm))))*(rhmsf1*rhmsf2)
kpfdfc<-(kpffled*(sum(kpnm)/(sum(kpnf)+sum(kpnm))))*(kpfsf1*kpfsf2)
kpfdmc<-(kpffled*(sum(kpnm)/(sum(kpnf)+sum(kpnm))))*(kpfsf1*kpfsf2)
kpfsfc<-(kpmfled*(sum(kpnf)/(sum(kpnf)+sum(kpnm))))*(kpmsf1*kpmsf2)
```

```
kpfsmc<-(kpmfled*(sum(kpnf)/(sum(kpnf)+sum(kpnm))))*(kpmsf1*kpmsf2)

A <-  matrix(c(0,0,rhfdf,0,0,rhfdm,0,0,0,0,0,0,
           rhfs11*rhfs12,0,0,0,0,0,0,0,0,0,0,0,
           0,(1-psi.rk)*rhfs21*rhfs22,rhfsa1*rhfsa2,0,0,0,0,psi.kr*kpfs21*kpfs22,0,0,0,0,
           0,0,rhfsf,0,0,rhfsm,0,0,0,0,0,0,
           0,0,0,rhms11*rhms12,0,0,0,0,0,0,0,0,
           0,0,0,0,(1-
psi.rk)*rhms21*rhms22,rhmsa1*rhmsa2,0,0,0,0,psi.kr*kpms21*kpms22,0,
           0,0,0,0,0,0,0,0,kpfdf,0,0,kpfdm,
           0,0,0,0,0,0,kpfs11*kpfs12,0,0,0,0,0,
           0,psi.rk*rhfs21*rhfs22,0,0,0,0,0,(1-psi.kr)*kpfs21*kpfs22,kpfsa1*kpfsa2,0,0,0,
           0,0,0,0,0,0,0,0,kpfsf,0,0,kpfsm,
           0,0,0,0,0,0,0,0,0,kpms11*kpms12,0,0,
           0,0,0,0,psi.rk*rhms21*rhms22,0,0,0,0,0,(1-
psi.kr)*kpms21*kpms22,kpmsa1*kpmsa2),
         byrow=T, nrow=12)

#simulation to estimate population growth rate when sex ratio not fixed: limited by rarer sex
#-------------------------------------------------------------------------------------------
Kk <- 200 # carrying capacity in king penguin colonies
Kr <- 250 # carrying capacity in rh penguin colonies
Tm <- 303 # length of time series
psi.kr <- 0
psi.rk <- 0
n0 <- c(rhfn0, rhmn0, kpfn0, kpmn0) # starting population values

n <- matrix(NA, nrow = length(n0),ncol=Tm)
n[,1] <- n0
rhmbp <-Kr/n[6]#breeding probability of rockhopper males

A <-  matrix(c(0,0,rhfdf,0,0,rhfdm*rhmbp,0,0,0,0,0,0,
           rhfs11*rhfs12,0,0,0,0,0,0,0,0,0,0,0,
           0,(1-psi.rk)*rhfs21*rhfs22,rhfsa1*rhfsa2,0,0,0,0,psi.kr*kpfs21*kpfs22,0,0,0,0,
           0,0,rhfsf,0,0,rhfsm*rhmbp,0,0,0,0,0,0,
           0,0,0,rhms11*rhms12,0,0,0,0,0,0,0,0,
           0,0,0,0,(1-
psi.rk)*rhms21*rhms22,rhmsa1*rhmsa2,0,0,0,0,psi.kr*kpms21*kpms22,0,
           0,0,0,0,0,0,0,0,kpfdf,0,0,kpfdm,
           0,0,0,0,0,0,kpfs11*kpfs12,0,0,0,0,0,
           0,psi.rk*rhfs21*rhfs22,0,0,0,0,0,(1-psi.kr)*kpfs21*kpfs22,kpfsa1*kpfsa2,0,0,0,
           0,0,0,0,0,0,0,0,kpfsf,0,0,kpfsm,
           0,0,0,0,0,0,0,0,0,kpms11*kpms12,0,0,
           0,0,0,0,psi.rk*rhms21*rhms22,0,0,0,0,0,(1-
psi.kr)*kpms21*kpms22,kpmsa1*kpmsa2),
         byrow=T, nrow=12)

for (i in 2:Tm) {
  n[,i] = A %*% n[,i-1]
```

```
 mmove.kr[i] <- ifelse(n[12,i-1]<Kk, 0, (n[12,i] - Kk))
 fmove.kr[i] <- ifelse(n[9,i-1]<Kk, 0, (n[9,i] - Kk))
 n[3,i] <- n[3,i] + fmove.kr[i]
 n[6,i] <- n[6,i] + mmove.kr[i]
 n[9,i] <- n[9,i] - fmove.kr[i]
 n[12,i] <- n[12,i] - mmove.kr[i]
 rhmbp[i] <- ifelse((Kr/n[6,i])>1, 1,(Kr/n[6,i]))
 rhfdf[i]<-(rhffled*min(c((n[3,i])/(n[3,i]+n[6,i])),((n[6,i])/(n[3,i]+n[6,i])))*(rhfsf1*rhfsf2) #rh
daughters by females
 rhfdm[i]<-(rhffled*min(c((n[3,i])/(n[3,i]+n[6,i])),((n[6,i])/(n[3,i]+n[6,i])))*(rhfsf1*rhfsf2) #rh
daughters by males
 rhfsf[i]<-(rhmfled*min(c((n[3,i])/(n[3,i]+n[6,i])),((n[6,i])/(n[3,i]+n[6,i])))*(rhmsf1*rhmsf2)
#rh sons by females
 rhfsm[i]<-(rhmfled*min(c((n[3,i])/(n[3,i]+n[6,i])),((n[6,i])/(n[3,i]+n[6,i])))*(rhmsf1*rhmsf2)
#rh sons by males
 kpfdf[i]<-(kpffled*min(c((n[9,i])/(n[9,i]+n[12,i])),((n[12,i])/(n[9,i]+n[12,i])))*(kpfsf1*kpfsf2)
#kp daughters by females
 kpfdm[i]<-(kpffled*min(c((n[9,i])/(n[9,i]+n[12,i])),((n[12,i])/(n[9,i]+n[12,i])))*(kpfsf1*kpfsf2)
#kp daughters by males
 kpfsf[i]<-
(kpmfled*min(c((n[9,i])/(n[9,i]+n[12,i])),((n[12,i])/(n[9,i]+n[12,i])))*(kpmsf1*kpmsf2) #kp
sons by females
 kpfsm[i]<-
(kpmfled*min(c((n[9,i])/(n[9,i]+n[12,i])),((n[12,i])/(n[9,i]+n[12,i])))*(kpmsf1*kpmsf2) #kp
sons by males
 rhfdfc[i]<-(rhffled*min(c((n[3,i])/(n[3,i]+n[6,i])),((n[6,i])/(n[3,i]+n[6,i])))*(n[3,i]) #for count
 rhfdmc[i]<-(rhffled*min(c((n[3,i])/(n[3,i]+n[6,i])),((n[6,i])/(n[3,i]+n[6,i])))*(n[3,i]) #for count
 rhfsfc[i]<-(rhmfled*min(c((n[3,i])/(n[3,i]+n[6,i])),((n[6,i])/(n[3,i]+n[6,i])))*(n[6,i]) #for count
 rhfsmc[i]<-(rhmfled*min(c((n[3,i])/(n[3,i]+n[6,i])),((n[6,i])/(n[3,i]+n[6,i])))*(n[6,i]) #for
count
 kpfdfc[i]<-(kpffled*min(c((n[9,i])/(n[9,i]+n[12,i])),((n[12,i])/(n[9,i]+n[12,i])))*(n[9,i]) #for
count
 kpfdmc[i]<-(kpffled*min(c((n[9,i])/(n[9,i]+n[12,i])),((n[12,i])/(n[9,i]+n[12,i])))*(n[9,i]) #for
count
 kpfsfc[i]<-(kpmfled*min(c((n[9,i])/(n[9,i]+n[12,i])),((n[12,i])/(n[9,i]+n[12,i])))*(n[12,i]) #for
count
 kpfsmc[i]<-(kpmfled*min(c((n[9,i])/(n[9,i]+n[12,i])),((n[12,i])/(n[9,i]+n[12,i])))*(n[12,i]) #for
count
}

#sum columns and plot
total1<- colSums(n)   #all subadults and adults
total2<-rhfdfc+rhfdmc+rhfsfc+rhfsmc+kpfdfc+kpfdmc+kpfsfc+kpfsmc   #all fledgers
total3<-total1+total2   #all birds

plot(total3, type='l',ylim=c(0,max(total3)), col='black')
lines(n[3,], col='red',lines(n[6,],col='blue',lines(n[9,], col='purple',lines(n[12,],
col='green',lines(total3)))))
```

```
(n[c(1,2,3,4,5,6,7,8,9,10,11,12),])
total3
```

Appendix F: Additional published work

The following work was done over the course of the thesis. However, the work was either led by a different author or not considered part of the current thesis. Nevertheless, it indicates additional academic endeavour in this field over the course of the thesis duration. The work is for the reader's interest, and does not form part of the thesis adjudication process.

Ornithological Observations

An electronic journal published by BirdLife South Africa and the Animal Demography Unit at the University of Cape Town

Ornithological Observations accepts papers containing faunistic information about birds. This includes descriptions of distribution, behaviour, breeding, foraging, food, movement, measurements, habitat and plumage. It will also consider for publication a variety of other interesting or relevant ornithological material: reports of projects and conferences, annotated checklists for a site or region, specialist bibliographies, and any other interesting or relevant material.

Editor: Arnold van der Westhuizen

EVIDENCE OF BREEDING BY DIVING PETRELS AND STORM PETRELS AT MARION ISLAND AFTER THE ERADICATION OF FERAL CATS

Gregory TW McClelland, John Cooper and Stephen L Chown

Recommended citation format:
McClelland GTW, Cooper J, Chown SL 2013. Evidence of breeding by Diving Petrels and Storm Petrels at Marion Island of the eradication of feral cats. Ornithological Observations Vol 4: 90-93

URL: http://oo.adu.org.za/content.php?id=89

Published online: 12 June 2013

- ISSN 2219-0341 -

EVIDENCE OF BREEDING BY DIVING PETRELS AND STORM PETRELS AT MARION ISLAND AFTER THE ERADICATION OF FERAL CATS

Gregory TW McClelland, John Cooper and Steven L Chown*

DST-NRF Centre of Excellence for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa

*Corresponding author: john.cooper61@gmail.com

The South African Prince Edward Islands, comprising Marion Island S46° 54', E37° 45') and the 21-km distant Prince Edward Island S46° 38', E37° 57', are among the most important sanctuaries for avifauna in the Southern Ocean. Twenty-nine species of bird have been recorded or are suspected to breed within the archipelago (Ryan and Bester 2008). Whereas the avifaunal community on near-pristine Prince Edward Island is considered to be essentially unaltered – it has never supported introduced predators – (De Villiers and Cooper 2008), Marion Island is likely still recovering from significant declines in its burrowing petrel populations as a consequence of four decades of predation by feral cats *Felis catus*.

Originally introduced to the Marion Island meteorological station in 1948 to control invasive House Mice *Mus musculus*, cats were first observed to have become feral and to feed on burrowing petrels in 1951/52 by RW Rand, the first biologist to make detailed observations of the island's birds (Rand 1954, Cooper 2008). They soon became well established around the entire island, having a deleterious effect on the island's bird populations. By 1977 cats were estimated to be taking approximately 455 000 burrowing petrels a year (Van Aarde 1980). It was not until 1991 that the last cat was killed after an eradication effort spanning 14 years (Bester *et al*. 2000, 2002). Improved breeding success was subsequently reported for some of the larger burrowing petrels (Cooper and Fourie 1991, Cooper *et al.* 1995) but much less is known about the fortunes of the smaller burrowing species.

Rand (1954) described Common Diving Petrels *Pelecanoides urinatrix* (first reported breeding on Marion Island in 1948; Crawford 1952) as "…widely distributed over the coastal plain where they burrow under tussock and moss near the cliff edge" in 1951/52. However, active burrows could not be located during the 1965/66 summer despite "extensive" searches in the same sites by Van Zinderen Bakker Jr (1971) or subsequently in 1979/80 by Schramm (1986), suggesting that they had been eradicated as a breeding species by feral cats at an early stage. South Georgia Diving Petrels *P. georgicus*, which prefer to breed at higher altitudes on Marion Island where they were "commonly found" (Rand 1954), were still being recorded ("Many nests…found" and "eleven…nests opened one day...containing birds incubating eggs") in 1965/66 by Van Zinderen Bakker Jr (1971). Although the habitat preferred by this species (described as cinder slopes) was not well surveyed during a 1979/80 burrowing petrel survey of the eastern portion of the island, "very few burrows were found" (Schramm 1986), suggesting that this species was also succumbing to predation by cats. These few nests (estimated as only 44 burrows in 21 ha) were the last known record of a diving petrel breeding on Marion Island for the next 32 years.

On 10 March 2011 GTWM found an active diving petrel burrow at S46° 51.736', E37° 42.839' near the cinder cone Tumor at an elevation of 552 m. The burrow entrance was located under an *Azorella selago* cushion among unvegetated scoria and contained a

Fig 1- Diving petrel chick on Marion Island, 10 March 2011.

partially downy chick weighing 70 g. Although photographed (Fig .1), the chick was not definitively identified to species, although the altitude and substratum suggests it was a South Georgia Diving Petrel.

On 16 March 2009 two juvenile Black-bellied Storm-Petrels *Fregetta tropica*, a species yet to be confirmed as breeding on Marion (Cooper and Brown 1990), were captured on the same night by GTWM near Fur Seal Peninsula on the western side of the island. Conditions were extremely foggy at the time and the birds collided with GTWM as a result of being drawn in by a head torch. Both birds came from the direction of the interior and had traces of down on their abdomens. It is most likely that they had very recently fledged from the island and that the species breeds there, although it is conceivable they could have come from Prince Edward Island, where breeding has been confirmed (Berruti *et al.* 1981, Imber 1983). Black-bellied Storm-Petrels with "bare vascularized brood patches and enlarged gonads" have been caught on Marion Island in the past (Williams and Burger 1978) and adults have been caught occasionally by spot-lighting at night in the vicinity of the meteorological station in recent years (Oceans & Coasts, Department of Environmental Affairs unpubl. records).

The Grey-backed Storm-Petrel *Garrodia nereis* has never been definitely reported breeding on Marion Island, although it has been on Prince Edward Island (Van Zinderen Bakker Jr 1971, Cooper and Brooke 1984). The species has also been caught ashore on Marion with vascularized brood patches and enlarged gonads (Williams and Burger 1978, see also Klages *et al.* 1995).

- oo0oo -

- ISSN 2219-0341 -

Acknowledgements

We thank the South African National Antarctic Programme, Department of Environmental Affairs for logistic support and the South African National Research Foundation for financial support via grant SNA2007044200003 to SLC. We thank RJM Crawford of the Department of Environmental Affairs for providing unpublished bird records. PG Ryan provided valuable comments that improved the manuscript.

References

Berruti A, Griffiths AM, Imber MJ, Schramm M, Sinclair JC 1981. The status of seabirds at Prince Edward Island. South African Journal of Antarctic Research 10/11: 31-32.

Bester MN, Bloomer JP, Bartlett PA, Muller DD, Van Rooyen M, Büchner H 2000. Final eradication of feral cats from sub-Antarctic Marion Island, southern Indian Ocean. South African Journal of Wildlife Research 30: 53-57.

Bester MN, Bloomer JP, Van Aarde RJ, Erasmus BH, Van Rensburg PJJ, Skinner JD, Howell PG, Naude TW 2002. A review of the successful eradication of feral cats from sub-Antarctic Marion island, southern Indian Ocean. South African Journal of Wildlife Research 31: 65-73.

Cooper J 2008. Human history. In: Chown SL, Froneman PW (eds). The Prince Edward Islands. Land-sea interactions in a changing ecosystem. SUN PReSS, Stellenbosch: 331-350.

Cooper J, Brooke MdeL 1984. Breeding status of burrowing petrels at Prince Edward Island. South African Journal of Antarctic Research 14: 34-35.

Cooper J, Brown CR 1990. Ornithological research at the sub-Antarctic Prince Edward Islands: a review of achievements. South African Journal of Antarctic Research 20: 40-57.

Cooper J, Fourie A 1991. Improved breeding success of Great-winged Petrels *Pterodroma macroptera* following control of feral cats *Felis catus* at subantarctic Marion Island. Bird Conservation International 1: 171-175.

Cooper J, Marais AVN, Bloomer JP, Bester MN 1995. A success story: breeding of burrowing petrels (Procellariidae) before and after the eradication of feral cats *Felis catus* at subantarctic Marion Island. Marine Ornithology 23: 33-37.

Crawford AB 1952. The birds of Marion Island, South Indian Ocean. Emu 52: 73-85.

De Villiers MS, Cooper J 2008. Conservation and management. In: Chown SL, Froneman PW (eds). The Prince Edward Islands. Land-sea interactions in a changing ecosystem. SUN PReSS, Stellenbosch: 301-330.

Imber MJ 1983. The lesser petrels of the Antipodes Islands, with notes from Prince Edward and Gough Islands. Notornis 30: 283-298.

Klages NTW, Nel DC, Cooper J 1995. Stomach contents of a Grey-backed Storm Petrel *Garrodia nereis* from Subantarctic Marion Island. Marine Ornithology 23: 163-164.

Rand RW 1954. Notes on the birds of Marion Island. Ibis 96: 173-206.

Ryan PG, Bester MN 2008. Pelagic predators. In: Chown SL, Froneman PW (eds). The Prince Edward Islands. Land-sea interactions in a changing ecosystem. SUN PReSS, Stellenbosch: 121-164.

Schramm M 1986. Burrow densities and nest site preferences of petrels (Procellariidae) at the Prince Edward Islands. Polar Biology 6: 63-70.

Van Aarde RJ 1980. The diet and feeding behaviour of feral cats, *Felis catus* at Marion Island. South African Journal of Wildlife Research 10: 123-128.

Van Zinderen Bakker Jr EM 1971. Comparative avian ecology. In: Van Zinderen Bakker Sr EM, Winterbottom JM, Dyer RA (eds). Marion and Prince Edward Islands. Report on the South African Biological & Geological Expedition /1965-1966. A.A. Balkema, Cape Town: 161-172.

Williams AJ, Burger AE 1978. Notes on nonbreeding seabirds at the Prince Edward Islands. Cormorant 5: 11-14.

Biological Conservation 161 (2013) 18–27

Contents lists available at SciVerse ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Human activities, propagule pressure and alien plants in the sub-Antarctic: Tests of generalities and evidence in support of management

Peter C. le Roux [a,1], Tshililo Ramaswiela [a,1], Jesse M. Kalwij [b], Justine D. Shaw [a], Peter G. Ryan [c], Anne M. Treasure [a], Gregory T.W. McClelland [a], Melodie A. McGeoch [d], Steven L. Chown [d,*]

[a] Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Matieland, South Africa
[b] Institute of Ecology & Earth Sciences, University of Tartu, 40 Lai Street, Tartu 51005, Estonia
[c] Percy Fitzpatrick Institute of African Ornithology, DST/NRF Centre of Excellence, University of Cape Town, Private Bag X3, Rondebosch 7701, South Africa
[d] School of Biological Sciences, Monash University, Victoria 3800, Australia

ARTICLE INFO

Article history:
Received 18 November 2012
Received in revised form 28 January 2013
Accepted 7 February 2013

Keywords:
Antarctic
Environmental change
Invasive alien species
Propagule pressure
Residence time

ABSTRACT

Despite concerns about the richness of plant invaders on islands, and their likely effects on local systems, impacts of these species seem to be small. However, this may be due to an absence of information on impacts, including changing species occupancy and forecast occupancy, rather than lack of impact per se. Here we use the plant invaders on the sub-Antarctic Prince Edward Islands (PEIs) and spatially explicit modeling of presence–absence survey data to demonstrate that the geographic extent of many invasives is increasing and is forecast to lead to occupancy of >60% of the islands' surface area by 2060, with ongoing climate change. In keeping with theory, proximity to human activity, neighboring populations (i.e. propagule pressure) and residence time, along with more minor contributors such as elevation, explain >50% of the variation in the occupancy of each of the six main invasive species on the islands. Human disturbance and changing climates seem to have led to recent increases in the rate of range expansion. Our results suggest that impacts of island plant invaders may be more significant than previously estimated, largely owing to prior data deficiency. More specifically they also suggest that control plans for the PEI (and other Southern Ocean Islands, SOIS) should first target less widely distributed species, which are invasive elsewhere. They also indicate that for the other SOIS, and for Antarctica, surveillance and anticipatory control plans should be in place.

1. Introduction

The introduction of non-indigenous species is a major cause of biodiversity change, especially on islands. These species modify diversity, alter ecosystem functioning, and often cause population declines (D'Antonio and Dudley, 1995; Blackburn et al., 2004; Pyšek et al., 2012). However, plant invaders are generally thought to be having less significant an impact on island systems than others such as mammals (compare Davis, 2003; Sax and Gaines, 2008 with Blackburn et al., 2004). Indeed, urgent calls for further investigation of island plant invaders have been made (e.g. Sax and Gaines, 2008). Vascular plants are the most species rich of the groups that have been introduced to and become invasive on the islands of the Southern Ocean, which are globally significant by virtue of their location, endemicity, and seabird populations (Convey and Lebouvier, 2009). Nonetheless, the extent of the impacts of invasive plants, by comparison with those of other taxa such as mammals, appears relatively minor (Frenot et al., 2005), and mostly indirect (Frenot et al., 2001; but see also Gremmen et al., 1998). Either the plant invasives are only having a minor impact, or the situation is a consequence of limited explicit investigation of the impacts of invasive plants across the region (for discussion see Vilà et al., 2010; Hulme et al., in press).

If impact for a given area is considered the product of the number of species that has undergone a transition from established to invasive, the range size (or average density or biomass) of each species, and effect per individual or unit biomass (see Parker et al., 1999; McGeoch et al., 2010), few assessments for the Southern Ocean Islands (SOIS) have indeed been made. Investigations of the number and identity of introduced vascular plant species per island are common (Bergstrom and Smith, 1990). However, assessments of changes in the status of species and in their geographic range are less widely undertaken (e.g. Gremmen and Smith, 1999; Scott and Kirkpatrick, 2005). For only one of the 25 SOIS

* Corresponding author. Tel.: +61 3 9905 0097; fax: +61 3 9905 5613.
E-mail address: steven.chown@monash.edu (S.L. Chown).
[1] These authors are contributed equally to the work.

0006-3207/$ - see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.biocon.2013.02.005

has a spatially explicit approach been used to document both gains and losses in area of occupancy (Frenot et al., 2001). Investigations of abundance and local impacts are less common still (Gremmen et al., 1998; Scott and Kirkpatrick, 2005).

Remedying this situation is of considerable conservation significance. If invasive plants are having minimal impact across the region, conservation spending might better be directed at other taxa, such as mammals, which do have significant impacts (Frenot et al., 2005). However, if the purported absence of impact is a consequence of limited investigation, impacts will accumulate until they can no longer be ignored, by that time likely being irreversible (Vilà et al., 2011; McConnachie et al., 2012). Perhaps for this reason, most SOIS management plans currently take a precautionary approach, recommending eradication of alien plants where feasible (de Villiers et al., 2005). However, control of plant invaders across the SOIS is uncommon, and has mostly been piecemeal, largely because the information required for prioritization and planning is absent (Grant et al., 2012). For the same reason, few generalities concerning the mechanisms underlying changes in invasion status (e.g. propagule pressure, residence time) have been developed across the region (unlike the case elsewhere – Křivánek et al., 2006; Gravuer et al., 2008), so further hampering invasion management (for general discussion see McGeoch et al., 2012), and failing to capitalize on an opportunity to test theory (e.g. Wilson et al., 2007) in a relatively remote system. Overall, the situation is not conducive to efficient conservation management, especially given forecasts of increasing invasion impacts for the SOIS (Frenot et al., 2005), and for Antarctica, which is prone to invasion by the same suite of species (Chown et al., 2012a).

Here we quantify the spatial distribution and local species richness patterns of introduced plant species at the sub-Antarctic Prince Edward Islands, as an exemplar system for the SOIS region. We model the factors explaining the current distribution and local richness of these species and, in conjunction with data from previous studies, estimate maximum rates of change in distributions on the islands. We also estimate: (1) the extent to which residence time has played a role in determining the current extent of invasion; (2) the likely equilibrium ranges of the species; and (3) the expected distributions of these species in 50 years' time given current rates of spread of each species and realized climate change (le Roux and McGeoch, 2008). In doing so we follow the useful development of such approaches applied to alien plant invasions in both continental and island settings (e.g. Schussman et al., 2006; Senan et al., 2012).

2. Methods

2.1. Site, species and residence time

The Prince Edward Islands (46°54′S, 37°48′E) comprise Marion Island (MI: 293 km^2, 1 230 m elevation) and Prince Edward Island (PEI: 45 km^2, 672 m elevation). They have a cool, oceanic climate and a tundra-type indigenous vegetation, varying from tussock grassland and mires in the lowlands to an impoverished polar desert at the higher elevations (Chown and Froneman, 2008). The islands were discovered in 1673, with the first documented landing in 1803/1804 (Chown and Froneman, 2008). Non-indigenous plants were first recorded in 1873 (*Cerastium fontanum* on MI; Moseley, 1874). In 1947 the islands were annexed by South Africa, with a continuous scientific presence since then on MI (Chown and Froneman, 2008). The first comprehensive survey of the vascular flora took place in 1965/1966 (Huntley, 1971), and biological research has since been continuous (Chown and Froneman, 2008), with the development of a network of field accommodation (huts) around MI in the 1970s (Fig. 1). Human activity on MI peaked during the feral cat, *Felis catus* L., eradication programme (1986–1991), involving many field workers moving between the huts and the research station. Prince Edward Island is less commonly visited and now has a higher conservation status than MI (de Villiers et al., 2005).

Seventeen non-indigenous vascular plant species have been introduced to and are currently established on MI, although some are of uncertain status (Table 1). Only three non-indigenous species have been recorded on PEI, all of which are still present (Ryan et al., 2003). Since Huntley's (1971) first assessments, comprehensive surveys of the alien vascular plant species on MI have been undertaken on a sporadic basis (Gremmen, 1975, 1981; Bergstrom and Smith, 1990; Gremmen and Smith, 1999), with fewer assessments for PEI (Bergstrom and Smith, 1990; Ryan et al., 2003; Table A1). Several of the previous studies have been comprehensive, with the authors suggesting that the spatial distributions of the species were well documented (Gremmen and Smith, 1999: 407; Ryan et al., 2003: 556).

To assign a year of first detection to each species we examined the literature on non-indigenous vascular plants recorded on the islands, and confirmed previous herbarium records (at Royal Botanical Gardens, Kew, UK). However, for most species, the first year of detection may not reflect the year of establishment owing to the absence of previous surveys (e.g. species recorded by Huntley, 1971) and to the taxonomic difficulty of some groups (Gremmen and van der Meijden, 1995). Thus, residence times (first year of this study (2006) minus year of first detection) should be considered a minimum estimate (Wonham and Pachepsky, 2006).

2.2. Surveys

Data from previous surveys (Table A1) were considered representative of the occurrence of the species unless the authors of the works either suggested that this was not the case or indicated that previous studies may have been so compromised (see Gremmen and Smith, 1999). In previous studies, the occurrence data for many of the species were either described by location or presented as mapped extents of occurrence (*sensu* Gaston, 1990) (e.g. Bergstrom and Smith, 1990; Ryan et al., 2003). Locality data from these studies were digitized (ARcGIS 9.3.1, ESRI, California) as presence data at a 0.5 × 0.5 min (hereafter half-minute) grid resolution (~926 × 635 m). This was done separately for each species, each of the islands and each of the years for which data were available (Table A1). Although the more cryptic species (e.g. *Agrostis castellana*) may have gone undetected, we made the assumption that the previous data represented a reasonable estimate of true absence. That is, at least since Gremmen's (1975) assessment, the now digitized data could be considered a minimum assessment of area of occupancy (Gaston, 1990) at a half-minute grid resolution for each species. Although such an assumption is complicated by the fact that the original occurrence maps may have included some half-minute grids unoccupied by the species concerned, the relationship between area of occupancy and extent of occurrence is typically strong (Gaston, 1990). Moreover, we selected the half-minute resolution to minimize this likely problem, acknowledging that resolution has an effect on estimates of occupancy (McGeoch and Gaston, 2002).

For the current survey, the half-minute resolution grid was retained for Marion Island. Over a period of 1 year (April 2006–May 2007) the center point of each grid was visited (below 500 m a.s.l., see Fig. 1 and Appendix 1) and a survey made of all non-indigenous vascular plant species within an 8 × 8 m square. Species absences were formally recorded, as was altitude, substrate type, vegetation type, aspect, and slope (see Chown and Froneman, 2008 for descriptions of substrate and vegetation types). As part of the survey protocol, all alien vascular plant species were also recorded *en route* to these sites. These '*ad hoc*' re-

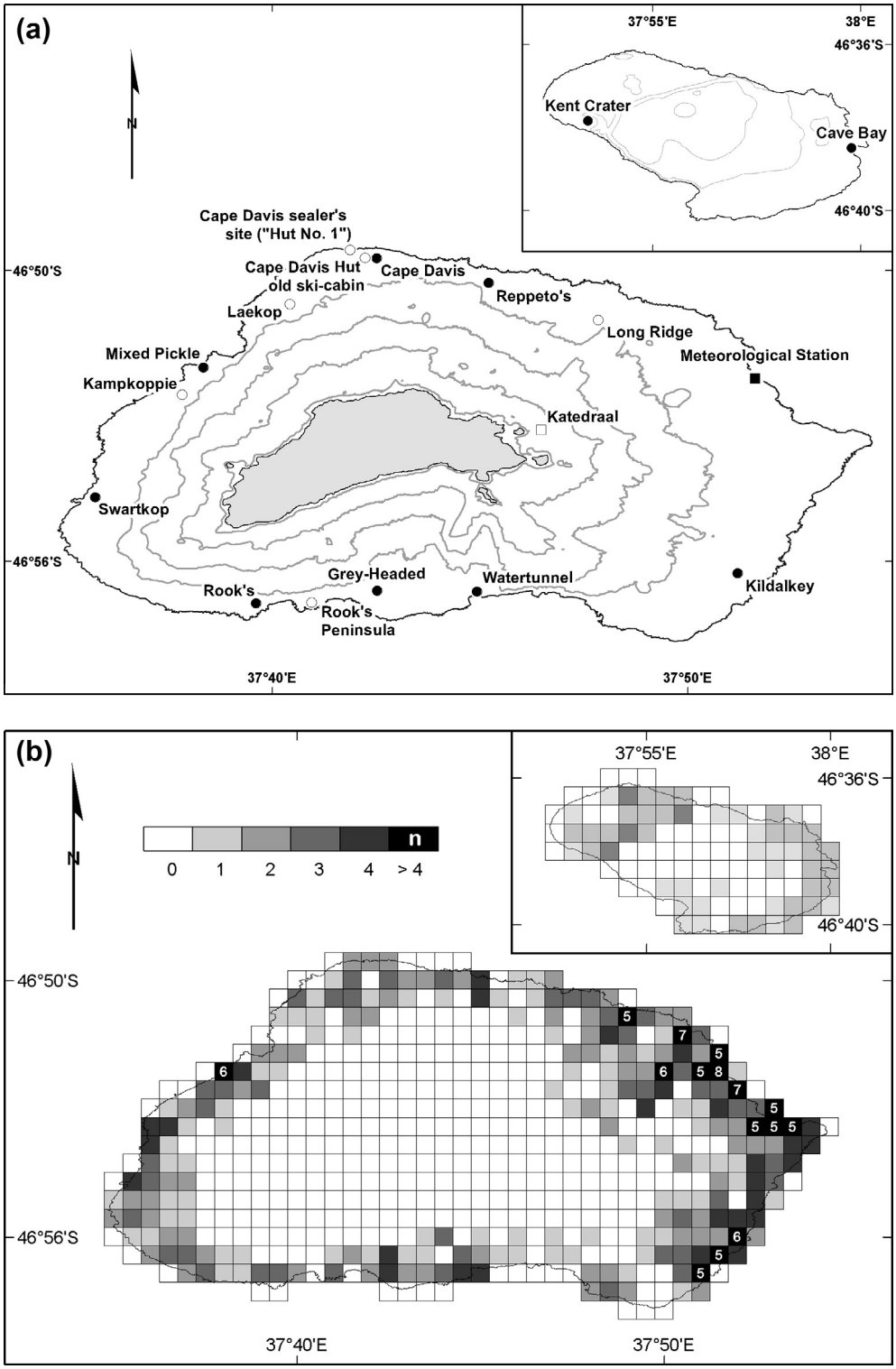


Fig. 1. (a) Topographic map of Marion Island indicating the location of the meteorological and research station (■; filled square), the contemporary field huts (●; filled circles), previous field hut sites (○; empty circles), and one contemporary, high-elevation field hut (□) that was excluded as a putative introduction site given that no indigenous vascular plants occur there. Areas above 840 m a.s.l., the current upper altitudinal limit to vascular plants, are shaded gray. In the inset, the location of two putative introduction sites (Cave Bay and Kent Crater) are mapped. On both maps, 200 m contour lines are plotted. (b) Alien plant species richness across Marion Island (Prince Edward Island in the inset) plotted at a half-minute resolution. Numbers in black cells indicate species richness when greater than four alien species.

cords were made by recording the species, spatial position (hand held GPS receiver, Garmin eTrex Vista, USA), and environmental variables as above, with additional information provided for large patches (Appendix 1). Spatial records were obtained for 2 317 unique localities (2 349 presence records across 14 species). Supplementary surveys for all areas including those above 500 m a.s.l. (Appendix 1) contributed a further 1 343 unique locations and 392 presence records.

The time available for surveys on Prince Edward Island was limited to 7 days in December 2008 (PGR/JDS/SLC) and 4 days in April

Table 1
The established, introduced vascular plant species found on the Prince Edward Islands, including details of original discovery, estimated original occupancy, occupancy based on data from this study, and rate of spread. Original occupancy is presented as the number of half-minute grid cells (~0.589 km^2) occupied when discovered, with more accurate estimates from the original (or a subsequent) source provided in parentheses where available. Current occupancy is also presented as the number of occupied half-minute grid cells, with an estimate of area provided in parentheses (for widespread species calculated as the number of cells multiplied by the total area of one half-minute grid cell; otherwise derived from the published literature or an estimate of patch size based on visual surveys). The species marked with an asterisk are of uncertain status and the mnemonics SS and WS refer to the suspected introduction either by sealers or following the establishment of the research station (after Chown and Froneman, 2008).

Species	Year discovered	Original collection or record attributable to	Estimated original occupancy (half-minute cells)	Estimated current occupancy (half-minute cells)	Rate of spread since discovery (km^2 year^{-1})
Marion Island					
Potamogeton nodosus Poir.*	1965	B.J. Huntley	1	1	0
Elymus repens (L.) Gould	1965 SS	B.J. Huntley	1 (250 m^2)	1 (250 m^2)	0
Agrostis castellana Boiss et Reut.	1975	N.J.M. Gremmen	2 (2 sites)	Unknown[a]	Unknown
Agrostis gigantea Roth	1994 WS	N.J.M. Gremmen	1 (<200 m^2)	1 (<200 m^2)	0
Agrostis stolonifera L.	1965	B.J. Huntley	1	40 (23.6 km^2)	0.56
Alopecurus geniculatus L.	1965 SS	B.J. Huntley	1 (<1 m^2)	1?	0
Festuca rubra L.	1965 SS	B.J. Huntley	1 (<100 m^2)	1 (<100 m^2)	0
Poa annua L.	1948 SS	Dike	1	147 (86.6 km^2)	1.48
Poa pratensis L.	1965 WS	B.J. Huntley	1	21 (12.4 km^2)	0.29
Juncus cf. effusus L.*	1965	B.J. Huntley	1	3 (1.8 km^2)	0.03
Luzula cf. *multiflora* (Retz.) Lej.*	1999	M.N. Bester & B. Stewart	1	2 (1.2 km^2)	0.08
Cerastium fontanum Baumg.	1873 SS	H.N. Moseley	1	155 (91.3 km^2)	0.68
Sagina procumbens L.	1965 WS	B.J. Huntley	1	129 (76 km^2)	1.84
Stellaria media (L.) Vill.	1873 SS	H.N. Moseley	1	31 (18.3 km^2)	0.13
Rumex acetosella L.	1953 SS	J.J. Van der Merve	1	2 (1.2 km^2)	0.01
Unidentified shrub*	2004	V.R. Smith	1 (one plant)	1 (one plant)	0
Prince Edward Island					
Poa annua	1966 SS	B.J. Huntley	1	16 (9.4 km^2)	0.22
Cerastium fontanum	1987	D.M. Bergstrom and V.R. Smith	1	7 (4.1 km^2)	0.19
Sagina procumbens	1997	N.J.M. Gremmen and V.R. Smith	1	37 (21.8 km^2)	2.36

[a] *A. castellana* cannot easily be distinguished from *A. stolonifera*, and its distribution is therefore assumed to be equal to or smaller than that of *A. stolonifera*. The grass *Holcus lanatus* was found in 2011 and is not listed here but only occurs at the meteorological station.

2010 (AMT/GM). In consequence, the half-minute resolution survey could not be undertaken. Rather, all previous sites at which alien species had been found were assessed and, during traverses for other work, the position of all occurrences of the three known alien species was recorded. In addition, 100, 1 × 1 m grid cells, haphazardly distributed across the island, were surveyed for the presence or absence of alien vascular plant species. No alien species new to the island were recorded. Additional absence records were generated from the GPS tracks of two observers (AMT/GM) who were recording alien species presences. Therefore, points on their tracks that were not presence records for these species reflect true absences (track points were reduced until all records were separated by at least 30 m). This provided a total of 1 181 unique localities and 215 presence records for the three alien species on Prince Edward Island.

2.3. Analyses

Survey data obtained above were rescaled to the half-minute grid resolution used for both islands for the previous survey data. Given the extent of the survey effort, unoccupied cells were considered real absences for mapping purposes and for the calculation of area of occupancy. The latter was calculated as the product of the number of grid cells occupied by each species and the area of each cell (*c.* 0.589 km^2). Change in occupancy was calculated per species as the difference in number of half-minute resolution grid cells occupied between two time periods (e.g. 2006 grids minus 1965 grids). The relationship between residence time and current occupancy for the species established on Marion Island was assessed using reduced major axis regression, with significance assessed through permutation (Legendre and Legendre, 1998).

To model the relationship between species occupancy and the environmental variables, presence and absence point data for the six widespread alien species on MI were analyzed using generalized linear models (GLM; spatially non-explicit) and generalized estimating equation models (GEE; spatially explicit) (see Bini et al., 2009 for rationale). Candidate predictor variables included altitude (as linear and quadratic terms because the altitude-diversity relationship is variable, Rahbek, 2005), vegetation type, substrate type, aspect and slope, a variable indicating the distance to the nearest population of the same species, and variables indicating distance from the research station and distance to the closest field hut (as two separate variables). Following a best subsets regression approach, all combinations of predictor variables were modeled. The resulting models were ranked by AIC (Akaike's Information Criterion; GLM) or QIC (quasi-likelihood-under-the-independence-model information criterion; GEE), after the exclusion of models with strongly collinear predictor variables (assessed with the variance inflation factor, VIF; Fox and Monette, 1992; Appendix 1). Analyses were repeated using a larger dataset, including records without vegetation, slope, aspect or substrate data (chiefly *ad hoc* records collected during other fieldwork). A best subsets approach was used again, with five candidate predictor variables (altitude, altitude^2, distance to closest field hut, distance to research station, distance to nearest conspecific population). The altitude^2 term was not included in models of *Agrostis stolonifera* distribution as it never gave a better fit than the linear altitude term and caused models not to converge.

Because MI is warming and drying with pronounced influences on the elevational range of many indigenous vascular plant species (le Roux and McGeoch, 2008), model assessments were also used to make qualitative predictions of further changes to the distribution of the six widespread alien species assuming a similar rate of climate change (and biotic response) over the next 50 years (recalling the possible effects of non-equilibrium conditions on model outcomes, Elith and Leathwick, 2009). The highest occurrence

and the 95th percentile of altitudes at which each species was recorded were used as two measures of the maximum elevations currently environmentally suitable for each alien species. Island area below each species' upper altitudinal limit was then summed (calculations based on a 20 m resolution digital elevation model; see Meiklejohn and Smith, 2008 and Appendix 1) as an estimate of the species maximum potential range. However, due to the scarcity of *Stellaria media*, *A. stolonifera* and *Poa pratensis* in fellfield vegetation and on scoria (present in less than 1% of records in fellfield vegetation; Table A2), their analyses were repeated after these habitat types were excluded.

All alien species presence records were used to calculate alien species richness across Marion Island in the 401 sampled half-minute grid cells. Eleven environmental variables were calculated for each grid cell (Appendix 1) and their relationship with species richness examined using GLM and spatial GEE models.

These analyses were repeated for Prince Edward Island. The distributions of its three alien plant species were modeled using GLM and GEE models, although fewer explanatory variables were available (altitude, altitude^2, the minimum distance to the nearest population of the same species, the distance to two putative introduction sites; Cave Bay and Kent Crater). Alien species richness across the island was also modeled using GLM and GEE models, acknowledging the small range of variation therein, with topographic parameters estimated from a digital elevation model (Appendix 1).

3. Results

3.1. Distribution and spread

Nine alien species have not increased their area of occupancy markedly or at all since their discovery (Table 1; Figs. A1 and A2). By contrast, six species have spread extensively. *S. media* is the one exception with an initial increase in area of occupancy and subsequent decline (Fig. 2). *Luzula* cf. *multiflora* has spread, but not sufficiently to extend beyond two grid cells. At present, *C. fontanum*, *P. annua* and *Sagina procumbens* are the most widespread species, with *S. procumbens* having the fastest rate of spread (Table 1 and Fig. 3).

3.2. Correlates of species distributions

For MI, the best models for the occupancy of the six most widespread alien species, using the extended dataset, all included nearest conspecific population: the likelihood of a species presence increases significantly with proximity to other individuals of the same species (Table 2). Some measure of altitude was also included in all models, although its negative effect typically was weak. The likelihood of presence was predicted consistently by the proximity of the research station and field huts in a smaller group of species, viz. *C. fontanum*, *P. annua*, and *P. pratensis*. In all cases, probability of presence declined with increasing distance from a human use

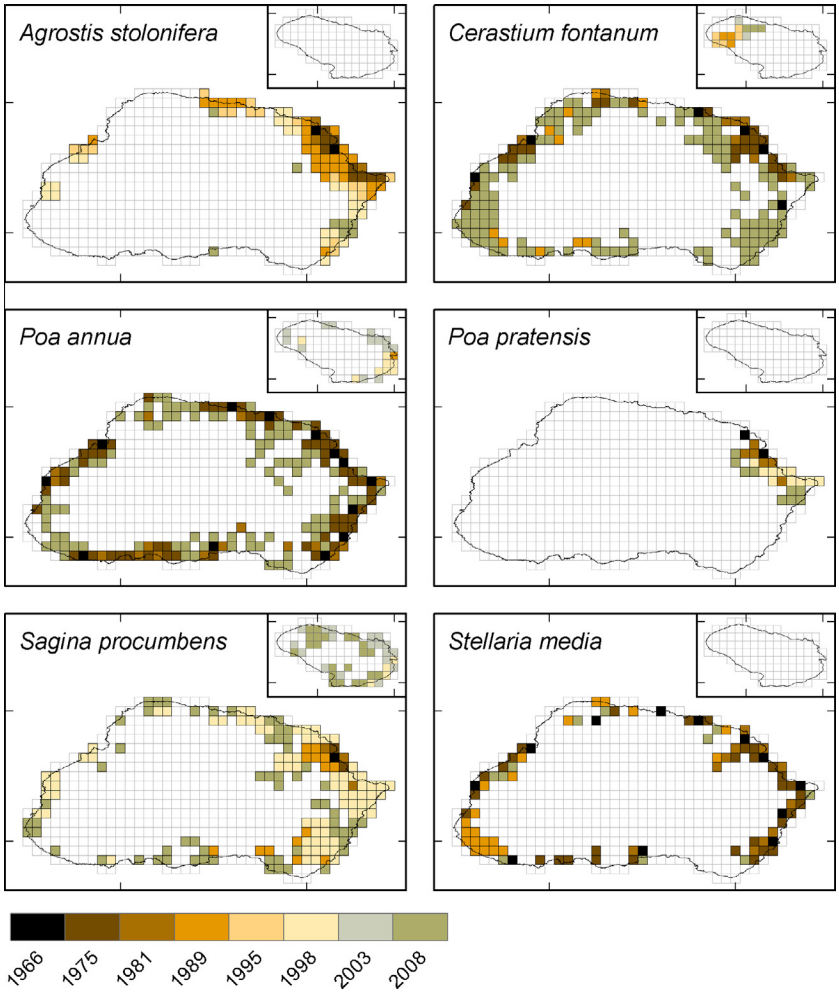


Fig. 2. Distribution of the six widespread alien vascular plant species on Marion Island (main figure) and Prince Edward Island (inset). Occupied half-minute grid cells are colored to indicate the year when the species was first recorded (see Table A1 for the details of previous surveys).

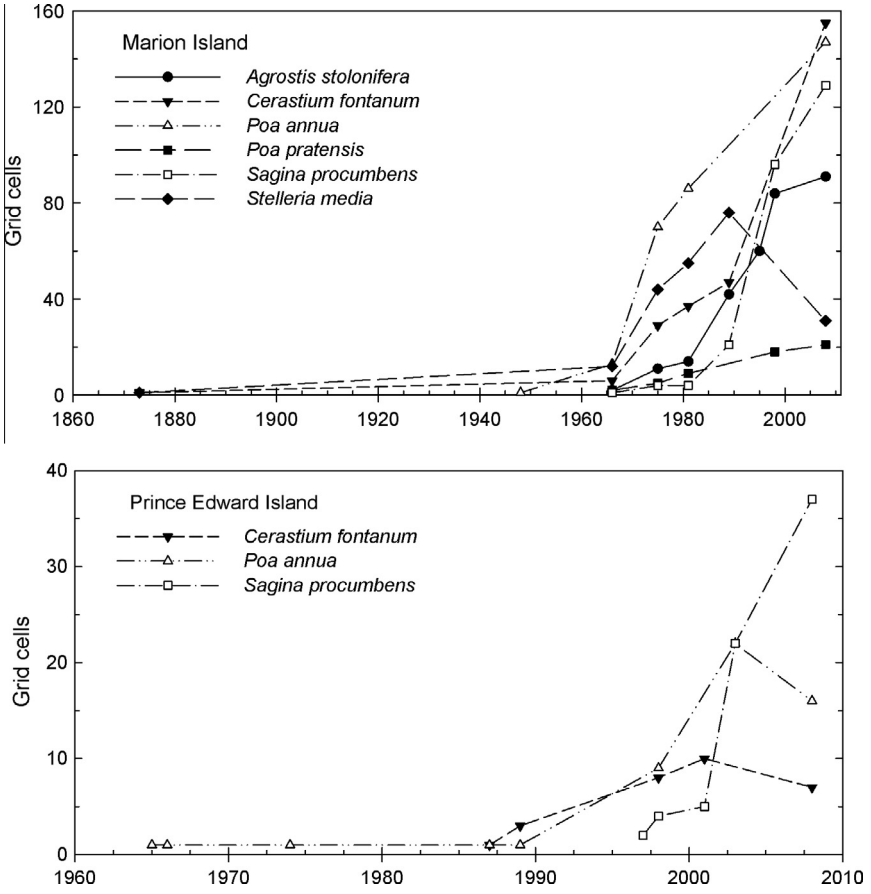


Fig. 3. Spread of the six widespread invasive alien species on Marion Island and Prince Edward Island. The number of occupied half-minute grid cells was set to one (i.e. 0.589 km^2) for the date of first recording (unless the first record indicated otherwise), although the species may well have been present before then and at the time of first recording may have been more widespread. Note that the lag phases of the species in common to the two islands are different in duration.

Table 2
Best fit generalized linear (GLM) and estimating equations (GEEs) models for the presence/absence of the six widespread alien vascular plant species on the Prince Edward Islands (see also Tables A5 and A6). The Akaike weight (AIC_w, or GEE equivalent, the QIC_w), adjusted D^2 (or equivalent measure of explained deviance for GEE models, the adjusted R^2) are shown for each model, together with the estimates of the coefficients of all the predictors retained in the best fit model. Coefficients differing significantly from zero are shown in bold.

Marion Island Species	Model	AIC_w (QIC_w)	Adj. D^2 (Adj. R^2)	n	Coefficient estimates					
					Intercept	Altitude	Altitude^2	NCP[a]	Base	Min. hut
A. stolonifera	GLM	0.37	0.61	1207	**1.745**	**−0.019**		**−6.226**		
	GEE	0.42	0.60	1207	**1.926**	**−0.021**		**−5.490**	−0.034	
C. fontanum	GLM	0.40	0.50	1227	**2.697**		**−0.00001**	**−5.319**		**−0.190**
	GEE	0.51	0.57	1227	**2.193**		**−0.00001**	**−4.949**	0.003	−0.104
P. annua	GLM	0.47	0.54	1165	**3.362**		**−0.00001**	**−5.824**	**−0.045**	**−0.217**
	GEE	0.55	0.62	1165	**2.962**		**−0.00001**	**−5.586**	−0.042	−0.150
P. pratensis	GLM	0.27	0.67	447	8.586		−0.00006	**−5.437**	**−0.405**	**−0.883**
	GEE	0.70	0.69	447	3.968		−0.00005	**−3.851**	−0.184	−0.347
S. procumbens	GLM	0.40	0.52	1580	**2.02**	**−0.004**		**−5.933**		
	GEE	0.53	0.61	1580	**1.68**	−0.001		**−6.033**		
S. media	GLM	0.19	0.43	906	0.188		−0.00003	**−2.062**		
	GEE	0.18	0.37	906	0.766	**−0.008**		**−2.072**		−0.084
					Intercept	Altitude	Altitude^2	NCP[a]	Kent Crater	Cave Bay
Prince Edward Island										
C. fontanum	GLM	0.20	0.79	1100	**4.724**			**−11.064**	**−0.949**	
	GEE	0.20	0.68	1100	5.491	0.009		**−10.918**	−0.805	−0.272
P. annua	GLM	0.29	0.60	1081	**1.403**			**−30.936**		**0.395**
	GEE	0.31	0.48	1081	1.287		<0.001	**−32.717**		**0.456**
S. procumbens	GLM	0.69	0.51	1120	**4.175**		**<0.001**	**−10.876**	**−0.527**	
	GEE	0.69	0.47	1120	−0.765	**0.009**		**−9.022**		**0.409**

[a] NCP = distance to nearest conspecific population, Base = distance to the research station, Min. hut = distance to the closest field research hut or the research station, Kent crater = distance to Kent Crater, Cave Bay = distance to Cave Bay (all measured in km).

area. The models typically explained more than 50% of the variation in the occupancy of the species, except for *S. media* where the explanatory power was lower. Differences between the GLM and GEEs in predictors included, variance explained, and the size and direction of the estimates were small.

Inclusion of slope, aspect, lava type and vegetation type data in the more restricted data set did not lead to large increases in the percentage deviance explained by the models (Table A3). Typically, the variables shared between this analysis and the previous one had the same sign and size. Although the additional variables often entered the best models, they frequently were not significant or had small effect sizes. Notable exceptions were for vegetation type in the case of *C. fontanum*, indicating a strong avoidance of salt-spray habitats and a preference for herbfield and mires, and for *Poa annua*, which avoids fellfield.

On Prince Edward Island, the species with the longest known history is *P. annua*, (Table 1). The occupancy of this species does not seem to have increased dramatically since 1966, and inter-survey variation likely reflects the extent to which the plant was actively sought by observers. In the models, distance to nearest conspecific population had significant negative effects, with a high proportion of the variance explained (48–60%; Table 2). For *S. procumbens c.* 50% of the variance in the data could be explained, with nearest conspecific population and altitude entering the models significantly. Curiously, a positive relationship with distance from Cave Bay (an area designated for camping) was found, reflecting the fact that the species was first found distant from this site and is still not associated with it. This species is spreading the most rapidly on the island (Table 1, Fig. 3). *C. fontanum* is also spreading rapidly, and distance from Kent Crater (the original site of colonization) and the presence of conspecifics are both significant and strong contributors to the *c.* 70% of the variance explained by the models. The decline in 2010 (Fig. 3) reflects lower sampling coverage of the inaccessible western side of the island than in previous years.

3.3. Effect of residence time and predictions of future spread

A significant positive relationship between residence time and area of occupancy exists for the established alien species on Marion Island (RMA: slope (and 95% CI) = 2.1 (0.85–5.24), $n = 14$, $R^2 = 0.26$, $p = 0.038$ based on 999 permutations, Fig. A3).

Based on their current upper altitudinal limits and habitat preferences (Tables A2 and A4), the six most widespread alien plant species on MI could be expected to occur over at least 30–74% of the island given sufficient time for propagule transport (and an even larger proportion of PEI; Table 3). If the widespread alien species expand upslope for the next 50 years at the same rate as indigenous species have for the last 40 years, owing to climate change, then these invasives could potentially occupy 51–86% of the island by 2060 (Table 3).

3.4. Species richness

Alien species richness on MI is highest in the proximity of the research station and certain coastal field huts (Fig. 1b). The best fit models included terms for altitude, altitudinal variability (GEE only), area, number of localities sampled, distance to hut and research station, and alien richness in surrounding grid cells. Of these, neighboring alien richness was strongest (explaining 30–43% of variation alone). Both GLM and GEE models explained a similar proportion of variability in species richness (62–63%; Table 4). On PEI, mean altitude, range of altitude, number of presence records, and average and maximum surrounding alien richness were important predictors in both GEE (28% variance explained) and GLM (49% variance explained) models (Table 4; Fig. 1b). However, the spatially explicit model also included terms for altitudinal variability, number of localities sampled and distance to Kent Crater.

4. Discussion

Of the 17 non-indigenous vascular plant species currently established on the Prince Edward Islands, six have spread rapidly since their introduction, and can now be considered widespread. An early statistical generalization suggested that about 10% of established species spread to become problematic, acknowledging that variance about the relationship is to be expected (Williamson and Fitter, 1996). To date, the transition on MI has taken place in about 35% of the established species, much higher than the earlier

Table 3
The current and potential future ranges of the six most widespread alien plant species on the Prince Edward Islands, expressed as percentage of total island area. Three scenarios of species range expansion in response to further climate change (+50 years) were calculated, using two estimates of species current upper altitudinal range limits; the 95th percentile and the maximum altitude of species' observations. Three species occurring on Marion Island are currently absent (or very rare; Table A2) in fellfield and scoria vegetation types, and therefore calculations were repeated only for the portion of the island that is currently covered by suitable habitat types.

Island	Species	Current distribution[a]	Scenarios for future altitudinal range expansion[b]					
			No expansion		Conservative expansion		Liberal expansion	
			95th percentile	Maximum	95th percentile	Maximum	95th percentile	Maximum
Marion Island (293 km^2)								
	Agrostis stolonifera	7.2	17.0	37.9	31.3	47.9	41.9	57.1
	Cerastium fontanum	27.8	50.0	61.1	58.9	68.9	67.1	75.6
	Poa annua	26.4	45.7	69.4	55.0	76.1	63.5	82.2
	Poa pratensis	3.8	14.1	30.1	29.9	40.9	40.7	50.7
	Sagina procumbens	23.2	31.6	74.0	42.4	80.3	51.9	85.6
	Stellaria media	5.6	31.6	34.5	42.4	45.2	51.9	54.3
Prince Edward Island (45 km^2)								
	Cerastium fontanum	7.0	51.1	55.1	61.9	65.7	72.9	75.8
	Poa annua	16.0	39.5	55.7	53.3	66.3	63.4	76.6
	Sagina procumbens	18.0	51.9	73.2	62.2	83.3	73.1	94.5
Marion Island excluding fellfield, scoria cones and polar desert (suitable habitat: 70 km^2)								
	Agrostis stolonifera		49.1	94.7	82.6	99.9	98.3	100
	Poa pratensis		41.2	80.2	79.8	97.6	97.5	100
	Stellaria media		83.2	88.7	98.6	99.4	100	100

[a] Calculated at a resolution of half-minute grid cells.
[b] Calculated from the DEM (i.e. resolution of 20 m for Marion Island and 30 m for Prince Edward Island). No expansion = in-filling of present altitudinal range only; Conservative expansion = upper altitudinal limit increases by 1.7 m/year; Liberal expansion = altitudinal limit increases by 3.4 m/year. Altitudinal range expansion scenarios are based on observed upslope expansion by indigenous vascular plant species on Marion Island (le Roux and McGeoch 2008).

Table 4
Best fit models explaining alien vascular plant species richness on the Prince Edward Islands (see also Table A7). The Akaike weight (AIC_w, or its GEE equivalent, the QIC_w), adjusted D^2 (or the equivalent measure of explained deviance for GEE models, the adjusted R^2) are shown for each model, together with estimates of the co-efficients of all the predictors retained in the best fit model. Coefficients differing significantly from zero are shown in bold.

Island	Model	AIC_W (QIC_W)	Adj. D^2 (Adj. R^2)	n	Terms included	Coefficient estimate
Marion	GLM	0.054	0.62	401	Intercept	−0.350
					Minimum altitude of grid cell	**−0.005**
					Grid cell size	**0.0001**
					Number of localities sampled	**0.011**
					Mean alien plant richness in surrounding cells	**0.348**
	GEE	0.047	0.63	401	Intercept	−0.424
					Minimum altitude of grid cell	**−0.005**
					Mean topographic roughness index	0.015
					Grid cell size	**<0.001**
					Co-efficient of variation of altitude	−0.412
					Number of localities sampled with alien species present	**0.011**
					Distance to nearest hut	−0.016
					Distance to research station	0.004
					Mean alien plant richness in surrounding cells	**0.401**
Prince Edward	GLM	0.011	0.49	61	Intercept	**−1.016**
					Minimum altitude of grid cell	**−0.005**
					Number of localities sampled with alien species present	**0.065**
					Max. alien plant richness in surrounding cells	**0.472**
	GEE	0.004	0.28	61	Intercept	**−1.562**
					Minimum altitude of grid cell	−0.004
					Altitudinal range	−0.0004
					Mean topographic roughness index	0.008
					Grid cell size	0.000
					Co-efficient of variation of altitude	0.641
					Number of localities sampled	−0.011
					Number of localities sampled with alien species present	**0.089**
					Mean alien plant richness in surrounding cells	0.012
					Max. alien plant richness in surrounding cells	0.329
					Distance to Cave Bay	−0.030

generalization (see also Richardson and Pyšek, 2006). Elsewhere, residence time plays a role in the proportion of species that are likely to spread and become problematic (Wilson et al., 2007). This appears to be the case also for MI despite the short residence time of most species (probably since the establishment of the scientific station in 1947; Huntley, 1971; Gremmen, 1981). However, because spread has also been rapid at Prince Edward Island (where *S. procumbens* and *C. fontanum* have only recently established; Table 1), residence time may not be the only mechanism determining the current extent of alien species distributions.

Rather, the islands' ecosystems may provide ready opportunity for the transition between establishment and invasion. Why this might be the case is not clear. Several works have suggested that islands are not more invasible relative to mainland areas (Lonsdale, 1999; Sol, 2000). By contrast, others have shown that islands house more invasive alien species than mainland areas (Sax and Gaines, 2008; McGeoch et al., 2010), suggesting that the transition from established species to invasive might be commonly made on islands. Across the SOIS, a positive relationship exists between indigenous and alien plant richness (Chown et al., 1998), implying little role for biotic resistance. On islands elsewhere, a disturbance mechanism (such as habitat alteration) might plausibly be responsible for the success of invasive species (e.g. Case, 1996). By contrast, at the Prince Edward Islands, human disturbance is low, although disturbance by birds and seals (Chown and Froneman, 2008) is common. Nonetheless, our analyses suggest that human intervention may well play a role in the local spread of the species.

Among the correlates of occupancy for all of the species, nearest conspecific presence contributed significantly in all species, emphasizing the significance of propagule pressure, in keeping with many other studies (e.g. Lonsdale, 1999; Richardson and Pyšek, 2006; Lockwood et al., 2009; Spear et al., 2013). However, distance to a site of human activity, such as the research station or field huts on MI, was either significant or included in the best fit models for most of the species too. Thus, the colonization of typically undisturbed areas of the islands (i.e. the transition from established to invasive) has likely been facilitated by human activity. Human activity on MI is limited largely to movement on paths among field huts (Chown and Froneman, 2008). No other form of anthropogenic habitat disturbance takes place except in the immediate vicinity of the research station and to a much smaller extent at the field huts on MI. Thus, human influences appear largely to have been in the form of additional propagule pressure, especially given high human activity during the cat eradication programme on MI between 1986 and 1991 (Bester et al., 2002). At this time, activity during the summer months was more than double the average. In addition to the usual overwintering team (10–16 personnel), hunting teams of *c.* 16 persons, deployed in groups of two from the field huts and scientific station, operated continuously and traversed the island actively hunting, trapping and baiting cats (Bester et al., 2002). Such activity might easily have led to the dispersal of several of the alien species, especially given their propensity for adhering to clothing or becoming lodged in bags (Lee and Chown, 2009).

Potentially confounding this explanation is the fact that average annual temperature has increased and total annual precipitation declined at the island since the 1950s (le Roux and McGeoch, 2008). More significantly, the increase in temperature has been especially pronounced since the late 1970s. Warmer temperatures may have improved the probability of species establishing and reproducing successfully, leading to what appears to be a change in rate of spread in the 1980s. That species are also spreading rapidly on PEI, where human activity is virtually non-existent (Chown and Froneman, 2008), provides further support for this idea. In all likelihood, both mechanisms are operating.

Irrespective of the causes of the transition from established to widespread, it is clear that *A. stolonifera*, *C. fontanum*, *P. annua*, *P. pratensis*, and *S. procumbens* are all widespread and likely to spread further, both assuming a constant climate and factoring in on-going climate change. Indeed, with the latter it can be assumed that more than 50% of the islands' vegetated areas will support one or more of these species by 2060. These forecasts are in keeping with the assumption that weedy species will take up the diversity capacity made available by increasing temperatures in non-water-limited systems (Woodward and Kelly, 2008; Chown et al., 2012b), especially given that, on isolated islands, natural colonization rates are exceptionally low. A curious exception on MI is *S. media*, the only species showing a decline in range. Given its wide global distribution in temperate areas it might be expected to have continued spreading on MI. The only plausible explanation for its decline is that since the 1995 ban on the delivery of fresh produce to the island (de Villiers et al., 2005), it has been widely sought by the scientific teams as an edible fresh green vegetable. Its disappearance from much of the east coast close to the research station, but on-going presence on the more distant, and less visited west (Fig. 2), provides support for this explanation.

The current distributions of the alien species, and the rapid spread of some of them, suggest that management actions to limit further impacts should first focus on the single species that is now starting to spread rapidly, *Luzula* cf. *multiflora*. Eradication of the eight species that have not spread (Table 1), but could plausibly do so given their histories elsewhere (e.g. *Elymus repens* and *Rumex acetosella*, Holm et al., 1977), is also a priority. Eradication of the more widespread species may cause more disturbance than no action at all, given that human movement has been implicated in this study as a cause of spread.

In addition, surveillance for new species should be undertaken routinely, and prompt action taken following discovery (see Hughes and Convey, 2012 for an assessment procedure). Surveillance for new species arrivals on the less impacted Prince Edward Island should be accompanied by an anticipatory management plan. Whilst visits to Prince Edward Island have frequently included surveillance for new alien species (e.g. Ryan et al., 2003), where these have been found no immediate action has been taken, leading to a situation where the species are now too widespread for effective control.

More generally, our results suggest that *A. stolonifera*, *C. fontanum*, *Luzula* cf. *multiflora*, *P. annua*, *P. pratensis*, and *S. procumbens* are likely to become widespread on other Southern Ocean Islands, and/or Antarctica were they to be introduced there. *P. annua* is already known to have done so on many of the islands, is the most widespread plant invader in the region (Frenot et al., 2005), and has also now started spreading on the Antarctic continent (Chown et al., 2012a; Molina-Montenegro et al., 2012). On Possession Island (Crozet archipelago) and Amsterdam Island, several of these species have also spread extensively (Frenot et al., 2001). Their seeds also routinely appear as propagules in the clothing and gear of those visiting these islands and Antarctica (Chown et al., 2012a). These species should therefore be targeted for surveillance, especially in rapidly warming areas of the continent. Thus, active and ongoing screening of clothing, equipment and cargo is important. Indeed, given the efficacy of such procedures in locating and reducing propagule loads (Lee and Chown, 2009; Chown et al., 2012a), management interventions should focus on these surveillance and prevention activities, coupled with rapid response action plans. Protocols for such action in the Antarctic Treaty area have already been set out (Hughes and Convey, 2012). They now need to be developed into action plans that are accepted by the various bodies such as national conservation agencies and the Committee for Environmental Protection of the Antarctic Treaty, that are jointly responsible for the conservation of the region.

Acknowledgments

K.I. Meiklejohn provided the DEM for Marion Island. Adriaan Dreyer, Leshia Visagie, Rob Crawford, the complement of the *FRV Africana*, CHC helicopters, and the Department of Environment Affairs provided field support. Two reviewers provided helpful comments. This work was supported by National Research Foundation of South Africa Grants SNA2007042400003 and IRF2008071500012. JMK was supported by the European Regional Development Fund (Centre of Excellence FIBIR). ASTER GDEM is a product of METI and NASA.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2013.02.005.

References

Bergstrom, D.M., Smith, V.R., 1990. Alien vascular flora of Marion and Prince Edward Islands: new species, present distribution and status. Antarct. Sci. 2, 301–308.
Bester, M.N., Bloomer, J.P., Van Aarde, R.J., Erasmus, B.H., Van Rensburg, P.J.J., Skinner, J.D., Howell, P.G., Naude, T.W., 2002. A review of the successful eradication of feral cats from sub-Antarctic Marion Island, Southern Indian Ocean. S. Afr. J. Wildl. Res. 32, 65–73.
Bini, L.M. et al., 2009. Coefficient shifts in geographic ecology: an empirical evaluation of spatial and non-spatial regression. Ecography 32, 193–204.
Blackburn, T.M., Cassey, P., Duncan, R.P., Evans, K.L., Gaston, K.J., 2004. Avian extinction and mammalian introductions on oceanic islands. Science 305, 1955–1958.
Case, T.J., 1996. Global patterns in the establishment and distribution of exotic birds. Biol. Conserv. 78, 69–96.
Chown, S.L., Froneman, P.W. (Eds.), 2008. The Prince Edward Islands: Land-sea Interactions in a Changing Ecosystem. African SunMedia, Stellenbosch.
Chown, S.L., Gremmen, N.J.M., Gaston, K.J., 1998. Ecological biogeography of southern ocean islands: species–area relationships, human impacts, and conservation. Am. Nat. 152, 562–575.
Chown, S.L. et al., 2012a. Continent-wide risk assessment for the establishment of nonindigenous species in Antarctica. Proc. Natl. Acad. Sci. 109, 4938–4943.
Chown, S.L., le Roux, P.C., Ramaswiela, T., Kalwij, J.M., Shaw, J.D., McGeoch, M.A., 2012b. Climate change and elevational diversity capacity: do weedy species take up the slack? Biol. Lett. 9, 20120806.
Convey, P., Lebouvier, M., 2009. Environmental change and human impacts on terrestrial ecosystems of the sub-Antarctic islands between their discovery and the mid-twentieth century. Pap. Proc. R. Soc. Tasm. 143, 33–44.
D'Antonio, C.M., Dudley, T.L., 1995. Biological invasions as agents of change on islands versus mainlands. In: Vitousek, P.M., Loope, L.L., Adsersen, H. (Eds.), Ecological Studies. Springer, Berlin, pp. 103–121.
Davis, M.A., 2003. Biotic globalization: does competition from introduced species threaten biodiversity? BioScience 53, 481–489.
De Villiers, M.S., Cooper, J., Carmichael, N., Glass, J.P., Liddle, G.M., McIvor, E., Micol, T., Roberts, A., 2005. Conservation management at Southern Ocean Islands: towards the development of best-practice guidelines. Polarforschung 75, 113–131.
Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. Annu. Rev. Ecol. Evol. Syst. 40, 677–697.
Fox, J., Monette, G., 1992. Generalized collinearity diagnostics. J. Am. Stat. Assoc. 87, 178–183.
Frenot, Y., Chown, S.L., Whinam, J., Selkirk, P.M., Convey, P., Skotnicki, M., Bergstrom, D.M., 2005. Biological invasions in the Antarctic: extent, impacts and implications. Biol. Rev. 80, 45–72.
Frenot, Y., Gloaguen, J.C., Masse, L., Lebouvier, M., 2001. Human activities, ecosystem disturbance and plant invasions in subantarctic Crozet, Kerguelen and Amsterdam Islands. Biol. Conserv. 101, 33–50.
Gaston, K.J., 1990. Patterns in the geographical ranges of species. Biol. Rev. 65, 105–129.
Grant, S.M., Convey, P., Hughes, K.A., Phillips, R.A., Trathan, P.N., 2012. Conservation and management of Antarctic ecosystems. In: Rogers, A.D., Johnston, N.M., Murphy, E.J., Clarke, A. (Eds.), Antarctic Ecosystems. An Extreme Environment in a Changing World. Wiley-Blackwell, Oxford, pp. 429–525.
Gravuer, K., Sullivan, J.J., Williams, P.A., Duncan, R.P., 2008. Strong human association with plant invasion success for *Trifolium* introductions to New Zealand. Proc. Natl. Acad. Sci. USA 105, 6344–6349.
Gremmen, N.J.M., 1975. The distribution of alien vascular plants on Marion and Prince Edward Islands. S. Afr. J. Antarct. Res. 5, 25–30.
Gremmen, N.J.M., 1981. Alien vascular plants on Marion Island (subantarctic). CNFRA 51, 315–323.
Gremmen, N.J.M., Chown, S.L., Marshall, D.J., 1998. Impact of the introduced grass *Agrostis stolonifera* on vegetation and soil fauna communities at Marion Island, sub-Antarctic. Biol. Conserv. 85, 223–231.

Gremmen, N.J.M., Smith, V.R., 1999. New records of alien vascular plants from Marion and Prince Edward Islands, sub-Antarctic. Polar Biol. 21, 401–409.
Gremmen, N.J.M., van der Meijden, R., 1995. Introduced *Agrostis* species at sub-Antarctic Marion Island. S. Afr. J. Antarct. Res. 25, 85–86.
Holm, L.G., Plucknett, D.L., Pancho, J.V., Herberger, J.P., 1977. The World's Worst Weeds: Distribution and Biology. University of Hawaii Press, Honolulu.
Hughes, K.A., Convey, P., 2012. Determining the native/non-native status of newly discovered terrestrial and freshwater species in Antarctica – current knowledge, methodology and management action. J. Environ. Manage. 93, 52–66.
Hulme, P.E., Pyšek, P., Jarošík, V., Pergl, J., Schaffner, U., Vilà, M. in press. Bias and error in understanding plant invasion impacts. Trends Ecol Evol.
Huntley, B.J. 1971. Vegetation. In: Van Zinderen Bakker, E.M., Winterbottom, J.M., Dyer, R.A. (Eds.), Marion and Prince Edward Islands. Report on the South African Biological and Geological Expedition 1965–1966. A.A. Balkema, Cape Town, pp. 98–160.
Křivánek, M., Pyšek, P., Jarošík, V., 2006. Planting history and propagule pressure as predictors of invasion by woody species in a temperate region. Conserv. Biol. 20, 1487–1498.
le Roux, P.C., McGeoch, M.A., 2008. Rapid range expansion and community reorganization in response to warming. Global Change Biol. 14, 2950–2962.
Lee, J.E., Chown, S.L., 2009. Breaching the dispersal barrier to invasion: quantification and management. Ecol. Appl. 19, 1944–1959.
Legendre, P., Legendre, L., 1998. Numerical Ecology. Elsevier, Amsterdam.
Lockwood, J.L., Cassey, P., Blackburn, T.M., 2009. The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. Divers. Distrib. 15, 904–910.
Lonsdale, W.M., 1999. Global patterns of plant invasions and the concept of invasibility. Ecology 80, 1522–1536.
McConnachie, M.M., Cowling, R.M., van Wilgen, B.W., McConnachie, D.A., 2012. Evaluating the cost-effectiveness of invasive alien plant clearing: a case study from South Africa. Biol. Conserv. 155, 128–135.
McGeoch, M.A., Butchart, S.H.M., Spear, D., Marais, E., Kleynhans, E.J., Symes, A., Chanson, J., Hoffmann, M., 2010. Global indicators of biological invasion: species numbers, biodiversity impact and policy responses. Divers. Distrib. 16, 95–108.
McGeoch, M.A., Gaston, K.J., 2002. Occupancy frequency distributions: patterns, artefacts and mechanisms. Biol. Rev. 77, 311–331.
McGeoch, M.A., Spear, D., Kleynhans, E.J., Marais, E., 2012. Uncertainty in invasive alien species listing. Ecol. Appl. 22, 959–971.
Meiklejohn, K.I., Smith, V.R., 2008. Surface areas of altitudinal zones on sub-Antarctic Marion Island. Polar Biol. 31, 259–261.
Molina-Montenegro, M.A., Carrasco-Urra, E., Rodrigo, C., Convey, P., Valladares, F., Gianoli, E., 2012. Occurrence of the non-native annual bluegrass on the Antarctic mainland and its negative effects on native plants. Conserv. Biol. 26, 717–723.
Moseley, H.N., 1874. On the botany of Marion Island, Kerguelen's land and Young Island of the Heard group. J. Linn. Soc. (Bot.) 14, 387–388.
Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., Von Holle, B., Moyle, P.B., Byers, J.E., Goldwasser, L., 1999. Impact: toward a framework for understanding the ecological effects of invaders. Biol. Invas. 1, 3–19.
Pyšek, P., Jarošík, V., Hulme, P.E., Pergl, J., Hejda, M., Schaffner, U., Vilà, M., 2012. A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. Global Change Biol. 18, 1725–1737.
Rahbek, C., 2005. The role of spatial scale and the perception of large-scale richness patterns. Ecol. Lett. 8, 224–239.
Richardson, D.M., Pyšek, P., 2006. Plant invasions: merging the concepts of species invasiveness and community invasibility. Prog. Phys. Geogr. 30, 409–431.
Ryan, P.G., Smith, V.R., Gremmen, N.J.M., 2003. The distribution and spread of alien vascular plants on Prince Edward Island. Afr. J. Mar. Sci. 25, 555–562.
Sax, D.F., Gaines, S.D., 2008. Species invasions and extinction: the future of native biodiversity on islands. Proc. Natl. Acad. Sci. USA 105, 11490–11497.
Schussman, H., Geiger, E., Mau-Crimmins, T., Ward, J., 2006. Spread and current potential distribution of an alien grass, *Eragrostis lehmanniana* Nees, in the southwestern USA: comparing historical data and ecological niche models. Divers. Distrib. 12, 582–592.
Scott, J.J., Kirkpatrick, J.B., 2005. Changes in Subantarctic Heard Island vegetation at sites occupied by *Poa annua*, 1987–2000. Arct. Antarct. Alp. Res. 37, 366–371.
Senan, A.S., Tomasetto, F., Farcomeni, A., Somashekar, R.K., Attorre, F., 2012. Determinants of plant species invasions in an arid island: evidence from Socotra Island (Yemen). Plant Ecol. 213, 1381–1392.
Sol, D., 2000. Are islands more susceptible to be invaded than continents? Birds say no. Ecography 23, 687–692.
Spear, D., Foxcroft, L.C., Bezuidenhout, H., McGeoch, M.A., 2013. Human population density explains alien species richness in protected areas. Biol. Conserv. 159, 137–147.
Vilà, M., Basnou, C., Pyšek, P., Josefsson, M., Genovesi, P., Gollasch, S., Nentwig, W., Olenin, S., Roques, A., Roy, D., Hulme, P.E., 2010. How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. Frontiers Ecol. Environ. 8, 135–144.
Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y., Pyšek, P., 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecol. Lett. 14, 702–708.
Williamson, M., Fitter, A., 1996. The varying success of invaders. Ecology 77, 1661–1666.
Wilson, J.R.U., Richardson, D.M., Rouget, M., Procheș, Ș., Amis, M.A., Henderson, L., Thuiller, W., 2007. Residence time and potential range: crucial considerations in modelling plant invasions. Divers. Distrib. 13, 11–22.
Wonham, M.J., Pachepsky, E., 2006. A null model of temporal trends in biological invasion records. Ecol. Lett. 9, 663–672.
Woodward, F.I., Kelly, C.K., 2008. Responses of global plant diversity capacity to changes in carbon dioxide concentration and climate. Ecol. Lett. 11, 1229–1237.